OSTEOLOGY OF THE JURASSIC REPTILE CAMPTOSAURUS, WITH A REVISION OF THE SPECIES OF THE GENUS, AND DESCRIPTIONS OF TWO NEW SPECIES.

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INTRODUCTION.

Twenty-nine years have passed since Prof. O. C. Marsh and his assistants made the first discovery of camptosaurian remains in the Jurassic deposits of North America. During this period, with the exception of a number of short papers prepared at various intervals by Professor Marsh, little has been written concerning this interesting group of extinct reptiles. Their apparent neglect is no doubt due in large part to the dearth of material, for, despite the fact that the gathering of collections has been continued with increased activity during the past eleven years by representatives of the various scientific institutions of the United States, but little new camptosaurian material has been brought to light.

The fossils upon which the present paper is largely based were acquired by the U. S. National Museum through the U. S. Geological Survey, being contained in that part of the Marsh collection transferred to the Museum in 1900. The greater part of the material was in the same condition as when received from the field many years previous, and its preparation in so complete a condition, in view of its rarity, has been most gratifying. Not only are there many individuals represented, but the perfection of two of the skeletons throws much additional light on their structural characteristics, and it has been thought advisable to give here for the first time a detailed description of the osteological structure of the genus. This will be followed by a discussion of the species in anticipation of defining their more important characteristics. This work was made possible by the study of the types and other specimens contained in the collections of the Yale University Museum, which were generously placed at my disposal.

The most serious difficulty in the proper study of the type-specimens was due to their lack of preparation. It is hoped, however, that in the text and figures presented here a little has been added to our conception of a form long neglected.

I take this opportunity to express my appreciation of the assistance given me during the preparation of this paper. To Dr. George P. Merrill, head curator of the department of geology, U. S. National Museum, I am first of all indebted for making possible the arrangements for the preparation and study of this material, and I gratefully acknowledge the many privileges extended; to Prof. Charles Schuchert, of the Yale University Museum, I am under obligations for the generous manner in which he placed at my disposal the types and all other camptosaurian material contained in the collections under his charge. I also wish to thank Prof. R. S. Lull, of the same institution, for courtesies extended during my visit to New Haven. For the privilege of studying material and assistance rendered, I am grateful to Dr. W. D. Matthew and Mr. Barnum Brown, of the American Museum of Natural History, New York. I am also indebted to Mr. Norman Boss, of the U. S. National Museum, for efficient assistance in the preparation of material, and to Miss M. W. Moodey in the final preparation of the manuscript.

HISTORY OF THE DISCOVERY OF QUARRY NO. 13.

With the specimens upon which the present paper is based were found many of the original field labels, on which the locality is given as "Quarry No. 13 or No. 13½, 8 miles east of Como, Wyoming." A brief history of the discovery and methods employed in working this important deposit of fossil remains is here given on account of the perfection of many of the specimens found in the quarry. It has furnished the holotypes of *Camptosaurus dispar*, *C. nanus*, and the allied forms, *Dryosaurus altus*, besides a vast quantity of other material, chiefly pertaining to the Stegosauridæ, among which are the holotypes of *Stegosaurus sulcatus* and *Diracodon laticeps*.[a] In response to an inquiry made of Mr. W. H. Reed, of Laramie, Wyoming (the original discoverer), as to the history of the discovery of this deposit of fossils, he writes:

> In August, 1879, I could see the end of quarry No. 10, where the type of *Brontosaurus excelsus* Marsh was found, so I took one of my men, Mr. E. G. Ashley, and we started out east from the main bluff (or Como-bluff). On the fourth day of our search, in the afternoon, being in the lowest of the Jura bone horizon, we found some hollow bones in the wash and soon after discovered the quarry. The first bones to be taken up was a nearly complete skeleton of *Allosaurus*. After this skeleton had been taken out, we found large quan-

[a] Prof. R. S. Lull informs me that the holotypes of *Cœlurus fragilis* and *Morosaurus lentus* also came from this quarry.

tities of *Stegosaurus* and *Camptosaurus* bones. This quarry was entirely different from any other Jurassic quarry I have ever seen, the matrix being a fine quality of sand. * * * There were also numerous small tubes with an outer crust of calcite. These were nearly uniform in size and about one-half inch in diameter. There were no large dinosaur bones found in this quarry, but it seemed to be a favorite resort for the smaller species. * * * The quarry was cut through by two gulches, and that portion on the west side of the west gulch was called 13 west, that part between the gulches was 13 east, and that on the east side of the east gulch was 13½. This is as I started the work, and I believe Brown continued this plan. * * * I find in my old notebooks the original locations that were filed in 1879 in order to hold it from trespassers.

An inclosure in the above letter shows the quarry to have been located in the northeast quarter of section 5, township 22 north, of range 76 west, Albany County, Wyoming.

Under the supervision of Mr. Reed, at that time employed by Prof. O. C. Marsh, quarry No. 13 was worked for the remainder of the season of 1879 and during the summers of 1880, 1881, and 1882. In 1883 further excavations were made under the direction of Mr. J. L. Kenney, and in 1884, Mr. Fred Brown assumed charge of the explorations, which were continued uninterruptedly until the autumn of 1887, when the quarry was abandoned as exhausted.

PLAN OF WORK.

The fossils collected from quarry No. 13 prior to 1882 are now preserved in the collection of the Yale University Museum, while the specimens resulting from the later excavations (the expense of collecting having been defrayed by the U. S. Geological Survey) are now in the paleontological collections of the U. S. National Museum. Much of this material still remains in the original packages as collected from twenty-one to twenty-six years ago.

Rough sketch maps of the quarry were made by Reed, on which he indicated the relative positions of all of the important bones found. Unfortunately only a few of these are now available. Later Brown formulated a more detailed plan of recording the relative positions of the specimens uncovered. The quarry was divided (see fig. 1) into what he designated diagrams, beginning with No. 1 and ending with No. 13. In some cases it is found that one diagram represented a season's work, while in other instances several diagrams were worked out in one year, probably due to the varying number of fossils found in the different sections. The diagrams were subdivided into 2-foot squares and, the maps being platted on the scale of 2 feet to the inch, bones as found could be accurately located on them. Each bone or group of bones (when taken up in one block) was given a quarry number, the bones found in each diagram beginning with number 1 and continuing serially for all of the specimens in that section.

The number being placed on a label with the specimens, as well as on the map, the exact position of a bone in relation to those found

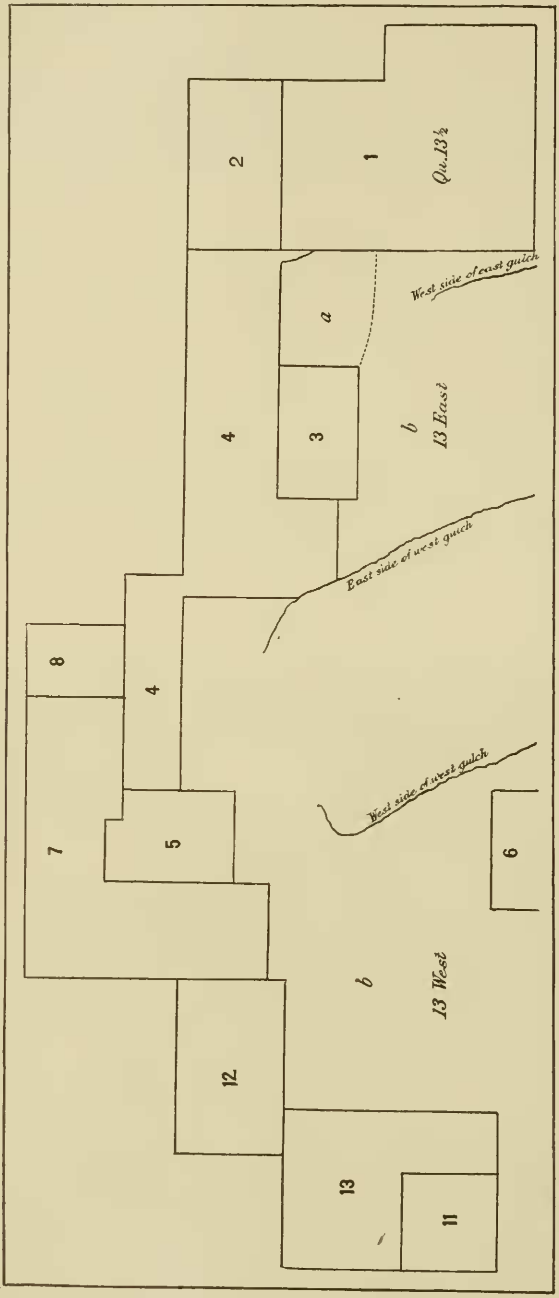


FIG. 1.—MAP OF QUARRY 13, SHOWING THE RELATIVE POSITIONS OF THE DIAGRAMS AS WORKED BY MESSRS. REED, KENNEY, AND BROWN FOR PROFESSOR MARSH, FROM 1879 TO 1887, INCLUSIVE. SCALE ABOUT 30 FEET TO THE INCH. *1*, *2*, *3*, AND *4*, DIAGRAMS ONE TO FOUR WORKED BY BROWN IN 1884; *5*, DIAGRAM FIVE, WORKED BY BROWN IN 1885; *6*, DIAGRAM SIX, WORKED BY BROWN; *7*, *8*, *11*, AND *12*, DIAGRAMS SEVEN, EIGHT, ELEVEN, AND TWELVE, WORKED BY BROWN IN 1886; *13*, DIAGRAM THIRTEEN, WORKED BY BROWN IN 1887; *a*, GROUND WORKED BY KENNEY IN 1883; *b*, GROUND WORKED BY REED IN 1879, 1880, 1881, AND 1882; *Qu.* 13½, IS ONLY RELATIVELY LOCATED, BEING ON THE EAST SIDE OF EAST GULCH. COMPILED FROM DIAGRAMS MADE BY MR. FRED BROWN.

near it could be quickly and accurately determined in the laboratory. Unfortunately a compilation of the several diagrams had never been made, and it was only after a most tedious search that the relative positions of those shown in fig. 1 were determined. There was no data found whereby diagrams 9 and 10 could be accurately located, and the area worked by Reed can only be indicated in a general way.

POSITION OF THE BONES OF CAMPTOSAURUS BROWNI AS FOUND IN THE QUARRY.

The most complete specimen considered in this paper is a new species, *Camptosaurus browni* (Cat. No. 4282, U.S.N.M.), which was collected by Mr. Fred Brown from quarry No. 13, 8 miles east of Como, Albany County, Wyoming, in 1885 and 1886. The accompanying map (see Plate 6) shows plainly how the bones of this individual were found as they lay embedded in the ground. The diagrams were drawn (as explained previously) at the time of disinterment, and the painstaking care bestowed on them is worthy of the highest commendation. Nearly a quarter of a century has elapsed since this skeleton was collected. During the interval the material from this area had become widely scattered, but by the aid of the diagrams the specimens were not only assembled, but I was enabled to again place all of the elements in their original relative positions.

Most of the skeleton lay in diagram 5, but a study of the contiguous area represented by diagram 7 showed other elements which could, beyond a reasonable doubt, be associated with the same individual, although collected a year later. The main axis of the skeleton lay in a northeast and southwest direction, and apparently not far removed from where the animal died.

As indicated by the original quarry numbers, the left fore limb and foot and anterior dorsal vertebræ were the first elements discovered. The limb and foot bones lay on the left side of the vertebral column in the positions indicated on the map (see Nos. 83, 84, and 85), the scapula and coracoid being removed some 5 feet to the left of the lower limb bones, but inasmuch as this is the only skeleton of *Camptosaurus* found in this part of the quarry, and as it pertains to the left side, there can be no doubt of their proper association. The vertebral column, which appears quite complete, was disarticulated at intervals. Beginning with the anterior portion of the backbone as preserved, cervicals 78, 77, and 76 were articulated by their zygapophyses and represent, respectively, the eighth and ninth cervicals and first dorsal. No. 83, although not interlocked with 78, was but little removed from it, and appears without question to represent the seventh cervical. Two other cervicals, No. 109 and another from which the original quarry number had been erased, are also provisionally associated with this skeleton, and represent the fourth and third cervicals, respectively. On account of the erasure of the quarry number the position of the third cervical could not be found on the map, although it was associated with the bones of No. 4282. The vertebræ of the next series, Nos. 101 to 106, while not interlocked by their zygapophyses, were so closely associated that there can be no question of their representing a series, and when prepared fit one another perfectly. The position of the capitular facets and shape of the spinous processes show them to pertain to the anterior dorsal region. An interval of a foot or more existed between No. 106 of this series and No. 76. In the next series, Nos. 120 to 136, the vertebræ were found occupying their relative positions and but little disturbed. From the adhering matrix I was able to connect up this series from the mid-dorsal through the sacral into the anterior caudal region, and an unbroken series is undoubtedly represented from the eighth dorsal back through the sacrals to the fourth caudal, inclusive. Caudals Nos. 168 to 169 and Nos. 158 and 159 were removed somewhat laterally, but were intermediate in size and appear to fill the gap between 136 and 170. Nos. 170 to 174, with their chevrons, were found articulated. Another series of four vertebræ (block 208) was shown in diagram 7, some 14 feet to the east of No. 174. But an anterior zygapophysis, retained in place by the matrix of the latter, was found to fit on the first vertebra of this series, and so fixed beyond doubt their proper position in the tail. Some 14 or 15 feet to the north and east another series of eighteen distal caudals (Nos. 218 to 235) was found, most of them articulated or so closely associated that it appears none are missing in the series.

It is perhaps fortunate that while the other bones found in this area represent the remains of several individuals, nearly all pertain to the genus *Stegosaurus*, from which the elements of *Camptosaurus* are readily distinguishable. This remark applies particularly to the rounded distal caudals of *Camptosaurus* which may at once be distinguished from the short hexagonal caudal centra of *Stegosaurus*. That this distal series belongs to *C. browni* there can be but little question. The ilia, Nos. 140 and 167, lay on their respective sides of the sacrum and but little removed from it, with their anterior ends directed forward. The other pelvic bones were not indicated on the map, but from their quarry numbers it was determined they could not have been far removed. Nothing of the hind limbs was found. The right fore limb (and foot) Nos. 98, 101, 119, and 120, were found to the west and right of the anterior cervicals. From the fact that all of the elements pertain to a right limb and closely agree in size with the left, its assignment appears certain. Some scattered ribs and pieces found near the dorsals have been provisionally associated with them. All of the remaining material from diagrams 5 and 7 has been gone over carefully in the hope of finding some elements of the skull and other missing parts, but without reward. It appears remarkable that in a skeleton which shows so little displacement of the elements as this one, that the heavy bones of the hind limbs should be missing. An unusual feature is the preservation of both fore limbs and feet. Experience of several seasons' field work has shown that while it is not unusual to find hind limbs fairly complete, the front legs, particularly of the Jurassic sauropods, are rare.

By reference to the quarry map (see Plate 6), all of the evidence as to the association of the parts may be plainly seen. The bones not numbered pertain to one or more genera different from *Camptosaurus*. The series to the east of the vertebral column represents a caudal series of *Stegosaurus*, and most of the other scattered elements have been recognized as belonging to that genus. With the exception of two caudal vertebræ, no duplicate bones of *Camptosaurus* have been found. There can be therefore little question but that all of the elements indicated as *Camptosaurus* belong to the one individual.

The position of the bones of the skeleton, as found in the quarry, is shown in diagrams 5 and 7, Plate 6. The position of the different parts is indicated by the original quarry numbers as follows:

IN DIAGRAM 5.

81. Dorsal rib.
83. Dorsal rib.
84. Left humerus.
85. Left radius, ulna, and manus.
98. Spinous process.
101 to 106. Dorsals (2, 3, 4, 5, 6, and 7 of series).
106. Thoracic rib.
107. Head of dorsal rib.
109. Piece of dorsal rib.
113. Portion of right ischium.
115. Left ischium.
116. Dorsal rib (portion of head).
120 to 128. Dorsals (8th to 16th of series).
129 to 133. Sacrals.
134 to 136. Caudals (1, 2, and 3 of series).
140. Left ilium.
157. Portion of dorsal rib.
158. Caudal (6th of series).
159. Caudal (5th of series).
167. Right ilium.
168. Caudal (3rd of series).
169. Caudal (4th of series).
170 to 174. Caudals (7, 8, 9, 10, 11, and 12 of series).
175, 176. Caudal vertebræ.
178. Chevron.

IN DIAGRAM 7.

45. Left scapula.
46. Left coracoid.
76. First dorsal.
77. Ninth cervical with one rib.
78. Eighth cervical with both ribs.
83. Seventh cervical.
84. Right humerus.
98. Right coracoid.
101. Right scapula.
109. Fourth cervical.
119. Right radius and ulna.
120. Right manus.
177. Ungual of Digit IV, right hind foot.
208. Caudals (13, 14, 15, and 16 of series).
218 to 235. Caudals (21st to 38th of series).

OSTEOLOGY OF CAMPTOSAURUS.

In the following pages an attempt is made to give a detailed description of the complete osteology of *Camptosaurus*, which, to a great extent, is based upon material preserved in the paleontological collections of the U. S. National Museum. This is supplemented, however, in many instances, and corroborated in others, by a study of the types and other specimens in the Yale University Museum, the collections of these two institutions containing the greater portion of the known *Camptosaurus* material from the Jurassic of this country.

Primarily the detailed description of the skeleton is based on Cat. No. 4282, U.S.N.M., holotype[a] of the new species, *C. browni*. I have selected this specimen on account of its representing a considerable portion of one individual, concerning the association of whose parts there can be but little question raised. Reference will occasionally be made to other individuals, where important structural differences are displayed, and bones not represented in this skeleton will be described from other specimens.

THE SKULL.

A complete articulated skull of *Camptosaurus* is unknown, although nearly all of its component parts have been recognized from the several disarticulated and fragmentary crania now preserved in the collections of the National and Yale museums.

Marsh was the first to attempt a restoration of the skull, which was based primarily upon the disarticulated elements of No. 1880 (holotype of *C. medius*), and the well-preserved anterior and posterior portions of No. 1887, Yale Museum, shown in Plates 7, 8, and 9 of the present paper. The latter specimen represents a very much larger individual, and, as suggested elsewhere, probably pertains to a distinct species. Thus the skull as figured could hardly be distinctive of *C. medius*, as formerly considered.

The restoration presented here (see figs. 2 and 3) is based upon the one given by Marsh, with such corrections and emendations as better preserved and more abundant material renders possible, and while it is anticipated that future discoveries will undoubtedly show the present restoration to be in error in some particulars, still it is believed that a clearer and more correct conception of the skull of *Camptosaurus* is given than could be obtained from the earlier representations.

[a] This is a term defined by Schuchert (Bull. U. S. Nat. Mus., No. 53, Pt. 1, 1905, p. 10): "A holotype in natural history is a particular individual deliberately selected by the author of a species, or it may be the only example of a species known at the time of original publication. A holotype, therefore, is always a single individual, but may embrace one or more parts, as the skin, skeleton, or other portions, such as the obverse and reverse of a natural mould."

The occipital region, parietals, and frontals have been largely based upon the posterior portion of a skull of *C. dispar*, No. 5473, U.S.N.M.

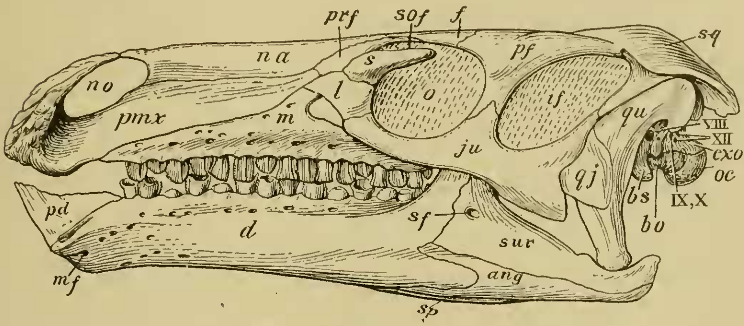


FIG. 2.—SKULL OF CAMPTOSAURUS. COMPOSITE RESTORATION; ABOUT ¼ NAT. SIZE. SEEN FROM THE LEFT SIDE; *ang*, ANGULAR; *bo*, BASIOCCIPITAL; *bs*, BASIPHENOID; *d*, DENTARY; *exo*, EXOCCIPITAL; *f*, FRONTAL; *if*, INFRATEMPORAL FOSSA; *ju*, JUGAL; *l*, LACHRYMAL; *m*, MAXILLARY; *mf*, MENTAL FORAMEN; *na*, NASAL; *no*, NASAL ORIFICE; *o*, ORBIT; *oc*, OCCIPITAL CONDYLE; *pd*, PREDENTARY; *pf*, POSTFRONTAL; *pmx*, PREMAXILLARY; *prf*, PREFRONTAL; *qj*, QUADRATOJUGAL; *qu*, QUADRATE; *s*, SUPRAORBITAL; *sf*, EXTERNAL MANDIBULAR FORAMEN; *sof*, SUPRAORBITAL FOSSA; *sp*, SPLENIAL; *sq*, SQUAMOSAL; *sur*, SURANGULAR; *VIII*, INTERNAL AUDITORY MEATUS; *IX*, *X*, FORAMEN LACERUM POSTERIUS; *XII*, HYPOGLOSSAL FORAMEN, AND FORAMEN FOR EXIT OF VEIN.

(see Plates 10 and 11). The anterior half as well as the infero-posterior part are after No. 1887, Yale Museum (see Plates 7 and 8).

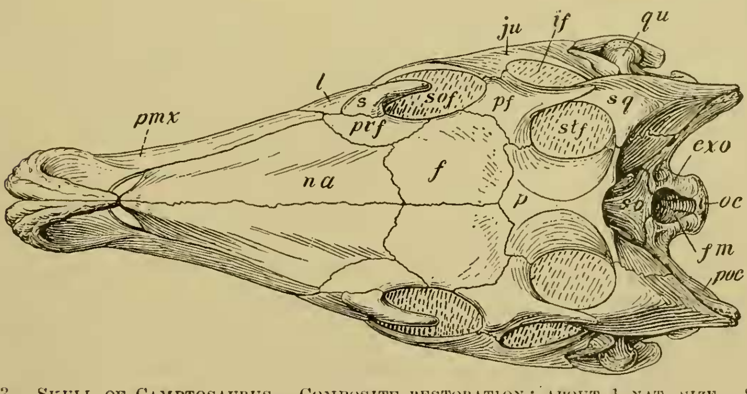


FIG. 3.—SKULL OF CAMPTOSAURUS. COMPOSITE RESTORATION; ABOUT ¼ NAT. SIZE. SEEN FROM THE TOP; *exo*, EXOCCIPITAL; *f*, FRONTAL; *fm*, FORAMEN MAGNUM; *if*, INFRATEMPORAL FOSSA; *ju*, JUGAL; *l*, LACHRYMAL; *na*, NASAL; *oc*, OCCIPITAL CONDYLE; *p*, PARIETAL; *pf*, POSTFRONTAL; *pmx*, PREMAXILLARY; *poc*, PARAOCCIPITAL PROCESS OR OPISTHOTIC; *prf*, PREFRONTAL; *qu*, QUADRATE; *s*, SUPRAORBITAL; *so*, SUPRAOCCIPITAL; *sof*, SUPRAORBITAL FOSSA; *sq*, SQUAMOSAL; *stf*, SUPRATEMPORAL FOSSA.

The lower jaw and maxillary are partly after No. 1887 and partly after No. 1886 (see figs. 7 and 8), also in the Yale Museum. No. 1880, although largely disarticulated, furnished much additional as well as corroborative information. A study of the disarticulated elements of several other individuals assisted greatly in the proper interpretation of their arrangement.

The predentary of *Camptosaurus* is as yet unknown, but as represented here is a modification of the *Iguanodon* type rather than of *Triceratops*, as first represented.

A restudy of the material now available has resulted in a number of modifications and changes, the more important of which may be briefly enumerated as follows:

(1) A more detailed presentation of the arrangement of the elements of the occipital and parietal segments.

(2) The removal posteriorly of the coronoid process of the mandible, which alters considerably the proportionate values of the dentary and the posterior elements of the jaw, that is, the lengthening of the former and shortening of the latter.

The many minor changes will be alluded to in more detail in the description of the elements to follow.

Viewed from above the skull is wedge-shaped, with the apex directed forward. When seen laterally it is of moderate depth, wider posteriorly than anteriorly, with a prominent orbit and large infratemporal fossa. The rami are moderately deep, but not so wide and heavy as in *Iguanodon*.

Basioccipital.—The heavy basioccipital is terminated posteriorly by the rounded occipital condyle, which is somewhat reniform in outline. In Cat. No. 5473, U.S.N.M., its greatest horizontal diameter is 40 mm. and its vertical diameter 25 mm. The smooth articular surface is continued forward on the under side of the condyle as a triangular area, the apex pointing anteriorly. The continuation of this articular surface would appear to indicate a greater mobility of the head up and down than from side to side, at the joint with the atlas. This would allow the anterior portion of the cranium to be considerably depressed.

In advance of the condyle the inferior surface is deeply concave longitudinally and convex transversely, with quite a pronounced median depression. Anteriorly and on either side of this depression are two blunt, roughened, basioccipital processes which abut against the expanded processes of the basisphenoid, the free extremities of which point downward and backward, and underlap those of the basioccipital. The basioccipital articulates with the basisphenoid by a median, tongue-like anterior extension, which is received in a corresponding notch on the posterior end of the latter, as in *C. prestwichii.* The intercalated basioccipital process on the ventral surface has a sharp median crest which begins behind in a depression in front of the condyle. The median superior surface is concave transversely and forms the floor of the foramen magnum. On either side of this depression are rough sutural surfaces for the exoccipitals, the posterior terminations of which enter slightly into the formation of the ball of the occipital condyle at its upper lateral corners.

Exoccipital and opisthotic or paraoccipital.—The exoccipitals form the greater part of the boundary of the foramen magnum and contribute slightly to the formation of the occipital condyle. Seen from behind, they rise as pillars from the condyle, articulating dorsally by oblique sutures with the supra-occipital, and continuing latero-posteriorly into the broad opisthotics or paraoccipitals. On the median posterior surface, just external to the lateral border of the foramen magnum, are pronounced circular depressions (see fig. 4). Dorsally, the paraoccipital appears to support the parieto-squamosal processes much as in *Stegosaurus*. The exoccipital and opisthotic are firmly coalesced, and there is no indication of the position of the suture, which evidently was early obliterated. On the inferior lateral surface of the exoccipital are four small foramina, one in front of another, the anterior one being separated from the other three by an oblique ridge. The more posterior pierces the exoccipital and enters the foramen magnum just within the external opening of the latter. As in *Morosaurus agilis*, *Diplodocus*, *Stegosaurus*, and *Triceratops*, this doubtless served to transmit the hypoglossal, or twelfth nerve; the next anterior which enters the foramen more inferiorly, instead of a branch of the twelfth nerve, as indicated in the figures, may have transmitted a vein, as in the crocodile; the third, which is separated from those posteriorly by a slight vertical ridge, was probably the exit for the pneumogastric and glossopharyngial nerves, while the fourth, the function of which is undetermined, passes diagonally through the outer anterior edge of the exoccipital and enters the large foramen just within its external opening. The nearly vertical suture between the opisthotic and prootic is plainly indicated on the portion of the skull of Cat. No. 5473, U.S.N.M. (see fig. 5). The broad paraoccipital processes extend outward and backward beyond the posterior termination of the condyle (see Plate 10, fig. 2). Viewed posteriorly (see fig. 4), the median part is con-

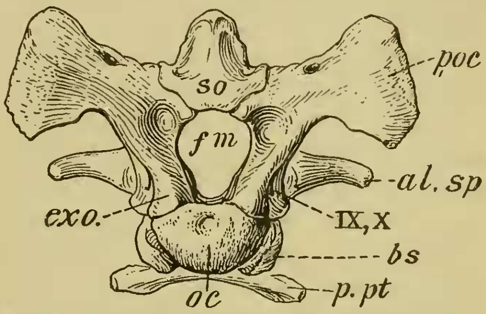


FIG. 4.—POSTERIOR VIEW OF OCCIPITAL REGION OF SKULL OF CAMPTOSAURUS DISPAR MARSH. CAT. NO. 5473, U.S.N.M.: $\frac{2}{3}$ NAT. SIZE. *Al. sp.*, ALISPHENOID; *bs*, BASISPHENOID; *exo*, EXOCCIPITAL; *fm*, FORAMEN MAGNUM; *oc*, OCCIPITAL CONDYLE; *poc*, PARAOCCIPITAL PROCESS OR OPISTHOTIC; *p. pt*, PROCESS ON BASISPHENOID WHICH MEETS THE PTERYGOID; *so*, SUPRAOCCIPITAL; *IX*, *X*, FORAMEN LACERUM POSTERIUS.

stricted, while the outer termination is expanded both dorsally and ventrally, more especially in the latter direction, into a wide, somewhat broadly rounded end. The posterior surface of this process is gently convex dorso-ventrally, while the anterior surface is plane, with a shallow, longitudinal groove extending for part of its length on the anterior inferior border.

Supraoccipital.—The supraoccipital of *Camptosaurus*, as in the English *Hypsilophodon* and *Camptosaurus prestwichii*, enters into the formation of the boundary of the foramen magnum. It contributes to the upper median boundary, and extends forward and upward into a stout pyramidal median crest, which is inclosed dorsally and laterally by the parietals. Ventrally it articulates by heavy sutured surfaces with the obliquely placed dorsal faces of the exoccipitals and prootics. The principal characters of this bone and the relation it bears to the surrounding elements of the skull are clearly shown in figs. 4 and 5.

Basisphenoid and parasphenoid.—The basisphenoid is very heavy and broad posteriorly where it articulates with the basioccipital by a deep vertical suture. On its posterior ventral surface two heavy, roughened buttresses are developed, which slightly underlap the anterior end of the basioccipital, and between which is received a heavy, median, tongue-like prolongation of the basioccipital. Anteriorly it is narrower and gives off a pair of diverging processes or pillars, produced somewhat below the ventral surface. These are directed downward, backward, and outward, and present in front at their extremities, surfaces for contact with the pterygoids (see *p*, *pt*, fig. 5). Latero-ventrally the basisphenoid is compressed, having laterally, one on either side, two forwardly directed slits, from which two converging foramini extend forward into the pituitary fossa. These foramini probably transmitted the carotid arteries, as in the crocodile (see *c*, fig. 5). They are also present in *Triceratops*, *Stegosaurus*, and *Iguanodon*. Dorso-laterally the basisphenoid articulates with the exoccipital, prootic, and alisphenoid. The parasphenoid extends forward from the base of the pituitary fossa as a median prolongation of the basisphenoid and divides the interpterygoid vacuity posteriorly into two parts. Its anterior extent, however, can not be determined from available material.

Alisphenoids.—The alisphenoids are a pair of roughly triangular bones which arise from the anterior dorsal surface of the basisphenoid, and unite dorsally as in the crocodile with the parietal, frontals, and postfrontals (see fig. 5). Their inner surfaces form the walls of that part of the brain case which lodges the cerebral hemisphere. Their anterior ends are divergent, turning decidedly outward, their dorsal surfaces being received in a transverse groove on the anterior ventral surface of the postfrontal. A narrow, posteriorly notched process descends to the basisphenoid a with it by a slightly expanded end. The posterior borde process forms the anterior margin of the foramen ovale fo transmission of the trigeminal or fifth nerve (see V, fig. 5.) Above the foramen ovale the alisphenoid is united by suture to the prootic bone, as plainly shown in Cat. Nos. 5473 and 5997, U.S.N.M. Their external surfaces form part of the inner and anterior boundaries of the supratemporal fossa. The alisphenoids in *Stegosaurus* appear to be identical in shape, position, and relationship, as regards the surrounding elements.

Orbitosphenoids.—Ossified orbitosphenoids were undoubtedly present, as indicated by two thin, flattened, plate-like elements found in the matrix with the alisphenoids of Cat. No. 5997, U.S.N.M. Furthermore, these appear (if not mutilated) to be large enough to complete the anterior portion of the brain case, as shown by specimen Cat. No. 5473, U.S.N.M. If present, they would form the walls which enclose the olfactory lobes of the brain.

The prootic.—Between the occipital and parietal segments of the skull of *Camptosaurus* is an area which must represent the position of the auditory or periotic capsule. As in most reptiles, the elements forming the capsules, i. e., the opisthotic and epiotic, are probably fused so that their exact identification is rendered somewhat difficult, the prootic alone remaining differentiated in the adult.

The prootic, as plainly shown by the two specimens, Cat. Nos. 5473 and 5997, U.S.N.M., is bounded as follows: Posteriorly by the opisthotic; dorsally by the supraoccipital, unless the epiotic be fused with that bone, a point, however, which can not now be determined; anteriorly by the alisphenoid, and ventrally by the basisphenoid. These relations are clearly shown in the specimens studied, as the sutures remain distinct in both.

In Cat. No. 5997, U.S.N.M., the prootic is all that remains of the lateral walls of the brain case, still attached to the basisphenoid, the alisphenoids, and orbito-sphenoids being present but detached from the rest of the specimen. As shown by a third specimen, No. 5996, U.S.N.M., these elements are united to the basisphenoid antero-posteriorly by pit-like, roughly sutured surfaces, but above they expand into a thickened wing-like dorsal portion produced more especially in the posterior direction, which extends backward and outward and laps along the median anterior surface of the outward extension of the opisthotic, uniting by horizontally striated sutural surfaces. Above the large foramen (internal auditory meatus, see VIII, fig. 5), the suture between the prootic and opisthotic is nearly vertical up to the backward projection of the former. The dorsal surface is united by an inclined sutural surface (see *s*, fig. 5) with the overlying supraoccipital. The figure shows the supraoccipital crushed upward from osition and thus exposes the ventral sutural surface in juxtaposition, would unite closely with the transversely ened dorsal surface of the prootic. Anteriorly it presents a thickened sutural surface for union with the alisphenoid. Below, the anterior border is deeply notched by the foramen ovale. The upper exterior surface forms part of the lower inner boundary of the supratemporal fossa. On the lower median part of the lateral surface is a deep, vertical groove leading up to a foramen entering the brain case, which, from its position, should represent the exit of the seventh or facial nerve. (See VII, fig. 5.)

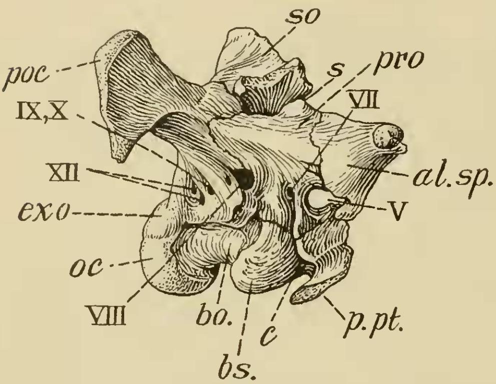


FIG. 5.—LATERAL VIEW OF POSTERIOR PORTION OF SKULL OF CAMPTOSAURUS DISPAR MARSH. CAT. NO. 5473, U.S.N.M.; 3/8 NAT. SIZE. *Al. sp.*, ALISPHENOID; *bo*, BASIOCCIPITAL; *bs*, BASISPHENOID; *c*, GROOVE LEADING TO FORAMEN THROUGH WHICH THE CAROTID ENTERS PITUITARY FOSSA; *exo*, EXOCCIPITAL; *oc*, OCCIPITAL CONDYLE; *poc*, PARAOCCIPITAL PROCESS OF OPISTHOTIC; *p, pt*, PROCESS FOR PTERYGOID; *pro*, PROÖTIC; *s*, SUTURAL SURFACE OF SUPRAOCCIPITAL, CRUSHED UPWARD FROM ITS NORMAL POSITION IN RELATION TO THE PROÖTIC WITH WHICH IT UNITES; *so*, SUPRAOCCIPITAL; *V*, FORAMEN OVALE; *VII*, FORAMEN FOR SEVENTH OR FACIAL NERVE; *VIII*, INTERNAL AUDITORY MEATUS; *IX, X*, FORAMEN LACERUM POSTERIUS; *XII*, HYPOGLOSSAL FORAMEN, AND FORAMEN FOR EXIT OF VEIN.

In the skull of *Triceratops*, Hatcher[a] was unable to distinguish the prootic, and in *Diplodocus*, Holland[b] did not detect its presence. In both cases the region which it should occupy if present was considered a part of the alisphenoid. From the facts brought out by a study of the skull of *Camptosaurus* which shows the presence of the otic elements in the dinosaurian skull, I believe they will be found in both of the forms mentioned above. In this connection it is of interest to quote from Huxley[c] who says: "The prootic is, in fact, one of the most constant bones of the skull in the lower vertebrates, though it is commonly mistaken, on the one hand for the alisphenoid, and on the other for the entire petro-mastoid."

The epiotic I am unable to recognize and if present, it occurs, as in most reptiles, fused with the supraoccipital, and no longer recognizable.

Parietal.—As in most reptiles (excepting *Chelonia*, *Ichthyosauria*, and some *Theromorpha*), the parietals in *Camptosaurus* are united. (See Plate 10.) An examination of two disarticulated skulls in which

[a] Mon. U. S. Geol. Survey, XLIX, 1907, p. 17.

[b] Memoirs Carnegie Museum, II, No. 6, 1906, p. 236, fig. 8.

[c] The Anatomy of Vertebrated Animals, 1872, p. 26.

all other sutures are distinctly seen, failed to show any indication of an interparietal suture. Hulke[a] has observed that *Hypsilophodon foxii*, *Iguanodon mantelli*, and *Camptosaurus* (*Iguanodon*) *prestwichii* all have unpaired parietals.

Seen from above the parietals are comparatively short, heavy bones. Their lateral surfaces, which form the upper walls of the brain case, are smooth, concave antero-posteriorly and thus constricted medially into a rounded crest, and without the sharp median sagittal ridge found in *Iguanodon*. Anteriorly the expanded end unites with the broad plate-like frontals by an angular suture. Laterally a prolongation of the anterior portion of the parietal curves outward to meet the postfrontals, and with these bones form the upper anterior boundary of the supratemporal fossa. Similarly the postero-lateral border turns outward, joining the squamosal with which it bounds posteriorly the upper opening of the fossa. Ventrally it encloses the upper portion of the supraoccipital. In the skull of *C. medius*, No. 1880, Yale Museum, the parietal has a transverse width of 51 mm. at its middle. There is no parietal (pineal) foramen in *Camptosaurus*.

Squamosal.—The following description of the squamosal of *Camptosaurus*, found among Professor Marsh's unpublished notes, is based on the left element of *C. medius*, No. 1880, Yale Museum.

> The squamosal fits very snugly on the head of the quadrate, and probably excludes the quadrate entirely from touching the paraoccipital process as in *Sphenodon*. In position it is most nearly related to that of *Iguana*. It has four distinct processes. The postfrontal process is very thin, flat, and arched outward above. The sutural surface is rather more than $1\frac{1}{2}$ inches in length, reaching to within a half inch of the tip of the quadrate. The head of the quadrate fits closely into a pit on the under surface. A slender process runs downward along the anterior exterior border of the quadrate containing the articulation for a third of the entire length. This corresponds in position to the same process on *Sphenodon* that runs down to articulate with the quadratojugal. In the present case it is much more slender and probably does not reach that bone.

The parietal process extends inward along the dorsal border of the paraoccipital process to meet the outward-turned process of the parietal, the two forming the upper posterior border of the supratemporal fossa as in *Stegosaurus*.

Frontals.—Viewed from above the paired frontals are irregularly five-sided bones, longer than wide, with a flattened, smooth dorsal surface. Posteriorly they unite with the parietal and postfrontals, and externally with the post- and prefrontals. The postfrontal border is convex instead of concave and extends anteriorly much farther than as first indicated by Marsh. The prefrontal border extends diagonally from the external border to the middle of the anterior end. A short, smooth surface between the anterior and posterior

[a] Phil. Trans. Royal Soc. London, CLXXIII, 1882, p. 1037.

extremities of the post- and prefrontals on the external border contributes to the inner boundary of the supraorbital fossa, but to no such extent as shown in Plate 53, fig. 2, in "Dinosaurs of North America." The orbital surface is large and concave antero-posteriorly in Cat. No. 5473, U.S.N.M., being separated from that of the opposite side by an intermediate space of 30 mm. The internal median ventral surface is separated from the orbital surface by an irregular, longitudinal ridge. This internal surface constitutes the roof of the anterior part of the brain case for the reception of the olfactory lobes.

Postfrontal.—The postfrontal is a three-rayed bone, and resembles that of the *Monitor* most nearly, but its union is chiefly with the frontals. One short, heavy ray articulates with the postero-external angle of the frontal and forms part of the anterior boundary of the supratemporal fossa. A slender, posteriorly directed ray articulates by a long, lapping suture with the anterior branch of the squamosal and with that bone completes the upper temporal bar which forms the outer boundary of the supratemporal fossa. The third ray, the longest of the three, unites by its strong descending process with the jugal and thus forms the posterior border of the orbit. This process below is trihedral in cross section.

Prefrontal.—The presence of a prefrontal is plainly indicated in two specimens in Yale Museum, Nos. 1880 and 1887. It is the lower external surface of this bone which gives the main support to the supraorbital and its posterior outer border forms a part of the internal boundary of the supraorbital fossa. This element, as preserved in the above specimens, is too mutilated for detailed description.

Quadrate.—I quote the following description from Professor Marsh's unpublished notes, kindly placed at my disposal by Prof. R. S. Lull, of Yale University Museum:

> The quadrate resembles most nearly that of *Iguana* but more slender. From the side the posterior border is concave and above the middle is rather thin. The posterior "hamalar" process of the head is quite thin. The surface for the pterygoid is large and hollowed and formed by thin bone. The articulation for the jaw is rectangular in outline and but slightly convex. From the front it is concave transversely throughout its whole length, deeply above, more shallow below.

Plate 9, fig. 2, shows the long, finger-like process of the pterygoid which extends backward and laps along a thin, forwardly directed process on the inner surface of the lower part of the quadrate. The quadrate in the skull of *C. medius*, No. 1880, Yale Museum, is 115 mm. in length. The external view of this bone is well shown in fig. 2, *qu*. In *Camptosaurus* the quadrate is more curved and lighter than the corresponding element in *Iguanodon*.

Quadratojugal.—The presence of this element is plainly indicated in specimen No. 1887, Yale University Museum (see Plate 8, *qj*).

It is a thin, subtriangular plate of bone which meets the jugal anteriorly by a curved but nearly vertical suture. The greater portion of this bone overlaps the median external surface of the quadrate. It is entirely excluded from the boundary of the infratemporal fossa by an ascending branch of the jugal.

Jugal.—The jugal is rather a wide bar posteriorly and is connected above with the descending process of the postfrontal and by an ascending process posteriorly with the quadratojugal and quadrate. It is not certainly known that this process reached the descending process of the squamosal as indicated in the restored skull. A curved, forwardly directed continuation of the jugal completes the lower boundary of the orbital opening, and undoubtedly articulates with the lachrymal, although this point could not be determined from actual observation. The above description is of the left jugal of No. 1887, Yale Museum.

Nasals.—The nasals are very large, subtriangular bones, which form a considerable part of the upper surface of the skull. They unite posteriorly with the frontals and prefrontals and laterally with the posterior process of the premaxillæ, and slightly with the prefrontal. Their concave anterior ends form most of the posterior boundary of the external nares. They terminate anteriorly on the median line as two points which meet the superior and posteriorly directed processes of the premaxillæ. In skull No. 1887, Yale Museum (see Plate 7), the suture separating the nasals is distinctly shown anteriorly.

Lachrymals.—The lachrymals are thin plates of bone wedged in between the maxilla, premaxilla, jugal, and prefrontal. They may have been slightly overlapped by the supraorbitals. They form part of the anterior boundary of the orbits. These bones were found *in situ* in specimen No. 1887, Yale University Museum (see Plate 7, *l.*).

Supraorbital.—The supraorbital has an expanded proximal articular end. Posteriorly it tapers rapidly to a small, nearly round extremity which remains free as in *Iguana.* The proximal end is roughened and deeply cleft, forming two surfaces which meet in the middle at an obtuse angle. When in position these faces are opposed to the lateral surfaces of the prefrontal and lachrymal (?), as shown in Plate 7. It forms the external boundary of the supraorbital fossa, as in *Iguanodon bernissartensis.* There is no indication of a posterior supraorbital in *Camptosaurus* as found in *Iguanodon.* In No. 1880, Yale Museum, the widest part of the supraorbital fossa was 14 mm. between the posterior end of the supraorbital and the exterior border of the frontal. Marsh's drawing of this region of the skull appears to be erroneous, as will be noticed by an examination of the reconstructed skull of *Camptosaurus medius*, in the Sixteenth Annual Report of the U. S. Geological Survey, Part II, Plate 53, figs. 1 and 2, the fossa being too large, and incorrectly designated as orbit.

Premaxillary.—Two specimens, Nos. 1880 and 1887, Yale Museum, have the premaxillæ preserved, and the following description is based upon their study:

In *Camptosaurus* the premaxillæ are edentulous. The dentigerous surface anteriorly is expanded transversely, but posteriorly it contracts and sends backward and upward a thin, flat process which is intercalated between the maxillary and nasal. The posterior termination appears to reach the prefrontal and has been so indicated in the restoration shown in fig. 2. I am inclined to believe it did not extend quite so far posteriorly as Marsh has indicated in his reconstruction of the skull.

A regularly curved subtriangular process rises from the anterosuperior surface and forms the upper boundary of the narial orifice. Medially it is closely applied to its fellow of the opposite side but not ankylosed. Thickened below, it gradually tapers upward to a point which meets the anterior extremity of the nasal at the summit of the external nares. The external surface of this process is very rugose and, like the rostral bone of *Triceratops*, was doubtless covered with a horny sheath which opposed a like covering over the predentary. At the base of this superior process is an oval foramen (see fig. 6, *f*), which pierces the bone, and appears on the ventral surface. The left premaxillary of No. 1880, Yale Museum, has a dentigerous surface 51 mm. in length. The greatest width of the expanded ends of the premaxillæ in this specimen is 41 mm. On either side of the median junction of the anterior ends are small rounded protuberances, separated medially by a shallow cleft.

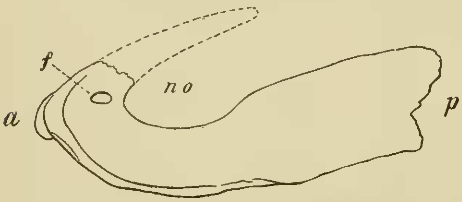


FIG. 6.—OUTLINE OF LEFT PREMAXILLARY OF CAMPTOSAURUS MEDIUS MARSH. NO. 1880, YALE MUSEUM; ½ NAT. SIZE. HOLOTYPE. *a*, ANTERIOR END; *f*, FORAMEN; *no*, NASAL ORIFICE; *p*, POSTERIOR END.

The principal characters of the premaxillary are well shown in Plate 7, fig. 1.

The maxillary.—As shown in fig. 7, the general outline of the maxillary is that of an irregular triangle. Dorsally it develops a slender, backwardly directed process which, in No. 1886, Yale Museum, rises to a height of 59 mm. above the external dentigerous margin. From the posterior base of this ascending process, the upper border gradually descends to 20 mm. above the last tooth.

Throughout nearly the whole length of the external surface, some 10 to 12 mm. above the border, the maxilla is pierced by a series of foramina. None of these, however, lead into the dental chamber but are received in a large, elongate cavity situated at the base of the dorsal process between the thin inner and outer walls, and which opens posteriorly. The foramina, in passing through the outer wall, are directed obliquely backward and appear to leave the maxillary posteriorly through a common channel or groove on the superior surface of the inner shelf-like projection of this part of the bone. This is well shown in the left maxillary of Cat. No. 5818, U.S.N.M. They probably transmitted the nerves and blood vessels leading to the lips. Above this row are still other irregularly placed foramina as shown in fig. 7. The slightly concave dentigerous surface in No. 1886 has alveoli for 16 teeth. In advance of the most anterior tooth a thin, flattened process is sent forward which underlies the posterior ascending process of the premaxillary. Viewed from above the maxillary remains about the same width throughout the median part, but the inner border of the posterior end is diagonally truncated. On the internal side just above the tooth row is another series of foramina which probably transmitted nerves and nourishment to the teeth.

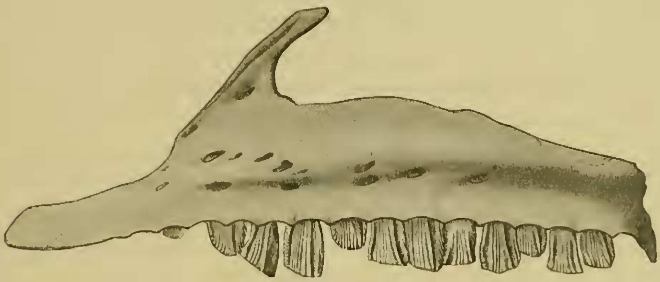


FIG. 7.—LATERAL VIEW OF LEFT MAXILLARY OF CAMPTOSAURUS. NO. 1886, YALE MUSEUM. ½ NAT. SIZE.

The exact relationships of the maxillary to the surrounding elements can not be determined further than what is shown in fig. 2.

EXTERNAL OPENINGS IN THE SKULL.

Foramen magnum.—The foramen magnum is large as compared with the size of the brain cavity, suboval in outline, being wider above than below, the longer diameter being vertical. It is bounded below by the basioccipital, on either side by the exoccipitals, and above by the supraoccipital (see fig. 4, *fm.*).

Supratemporal fossæ.—The supratemporal fossæ are situated one on either side of the parietals. They are bounded anteriorly by the postfrontals and parietals; internally by the parietals; posteriorly by parietals and squamosals; externally by the squamosals and a posterior prolongation of the postfrontals. These openings are proportionately much larger and more elongate than in *Stegosaurus.*

Supraorbital fossa.—The supraorbital fossa is bounded anteriorly by the prefrontal and supraorbital; posteriorly by the postfrontal;

externally by the inner surface of the supraorbital. It is not certainly known whether the external border was entirely closed by the development of a post-supraorbital as found in *Iguanodon bernissartensis*. So far as I am aware, *Camptosaurus* is the only American dinosaur having such a fossa. When skulls of *Laosaurus* and *Dryosaurus* are known, similar openings will probably be found.

Infratemporal fossa.—The infratemporal fossa is bounded above by the posterior branch of the postfrontal; behind by the descending process of the squamosal and ascending process of the jugal; below by the jugal, and in front by the ascending and descending process of the jugal and postfrontal, respectively. Proportionately this fossa has no such development as is found in *Iguanodon*, where it is greatly elongated dorso-ventrally.

There are no preorbital fossæ.

Orbital cavities.—As indicated by the extent of the orbital surfaces on the postfrontals of Cat. No. 5473, U.S.N.M., these cavities must have been of good size. Their exact contours, however, are somewhat problematical, as none of the cranii studied have the boundaries of the orbits intact, but, as interpreted, the reconstructed skull (see *o*, fig. 2), which was drawn after a careful study of all available material, is believed to be a fairly accurate representation of their shape and size. They are bounded above on the outer margin by the supraorbitals and postfrontals; behind by the descending process of the postfrontals and ascending process of the jugals; below by the jugals; in front by the jugals, lachrymals, and supraorbitals. There is no indication of a postorbital in *Camptosaurus*.

The narial opening.—The narial opening is well shown in No. 1887, Yale Museum (see Plate 7), after which this region of the figured skull was drawn. It is of good size, suboval in outline, with its greatest diameter inclined to the longer axis of the skull, as in *Iguanodon bernissartensis*. Excepting the posterior border, which is formed by the nasals, the remainder of the orifice is inclosed by the premaxillaries. Anteriorly, the roughened ascending process of the premaxillaries roof over somewhat the lateral openings.

Lesser foramina.—The well preserved posterior portion of the skull of Cat. No. 5473, U.S.N.M., shows with unusual clearness the smaller foramina of this region (see figs. 4 and 5). By a comparison with the foramina in other reptilian skulls of both fossil and recent forms, and by examining the relations of the various foramina to one another, it is believed they have been determined with a considerable degree of accuracy.

Beginning with the most posterior, we find on the lower lateral margin of the exoccipital a pit-like depression, from the bottom of which two foramina pierce the exoccipital, entering the brain case just within the external opening of the foramen magnum (see XII, figs. 2 and 5). In passing through the wall they diverge somewhat, their internal openings being 5 mm. apart, the anterior being the smaller and occupying a more ventral position. It was first thought that both of these foramina belonged to the hypoglossal, and I find that Andrews[a] has so interpreted similarly placed openings in the skull of *Iguanodon*, although he suggests that the spinal accessory may have occupied one. Hatcher[b] considers that in *Triceratops* the two posterior foramina transmitted the XII and XI nerves.

I am inclined to the opinion, however, that the second and more ventrally placed foramen was for a vein, as found in the living crocodile, the first being the true hypoglossal foramen (see XII, fig. 5). A few millimeters anterior to the opening for the twelfth nerve is a third foramen, shown IX and X, fig. 5, which is identified as the foramen lacerum posterius, through which the pneumogastric, vagus, and glossopharyngial nerves were transmitted. This foramen extends forward diagonally through the exoccipital, passing out on its anterior border into a large foramen (see VIII, fig. 5), between the exoccipital, opisthotic, and prootic, just before the latter enters the brain case. Externally the foramen lacerum posterius is separated from the foramina posteriorly by a weak vertical ridge, and anteriorly by a heavier rounded ridge which rises near the base of the exoccipital and extends diagonally upward and backward, fading out on the lower border of the paraoccipital process. Six millimeters anterior to the foramen lacerum posterius is another small foramen which passes through the antero-external corner of the exoccipital, and also opens into the large foramen mentioned above. Its function, however, is unknown.

From the position of the large foramen (VIII, fig. 5), bounded principally by the otic bones, I identify it as the internal auditory meatus, through which the auditory nerve leaves the cranial cavity and enters the internal ear. This interpretation appears to be approximated in the long, slit-like internal auditory meatus in extant Crocodila, which is also bounded by the opisthotic, prootic, and exoccipital. As in the crocodile, there is no ossified division of this opening into the fenestræ ovalis and rotunda.

Eight millimeters anterior to the internal auditory meatus, a small foramen pierces the median part of the prootic which is considered the exit of the seventh or facical nerve (see VII, fig. 5). Below, a deep, vertical depression leads up to this foramen from the slit-like fissure on the lateral border of the basisphenoid through which the carotid enters the pituitary body.

Huxley[c] writes that in all higher Vertebrata "the third division of the trigeminal or fifth nerve always leaves the skull behind the

[a] Annals and Magazine of Natural History, 6th ser., XIX, 1897, p. 590.

[b] Mon. U. S. Geol. Surv., XLIX, 1907, pp. 36, 37, fig. 31.

[c] Anatomy of Vertebrated Animals, 1872, p. 70.

center of the alisphenoid and in front of the pro-otic." Following this definition it locates at once the foramen ovale as the large opening (V, fig. 5) between the union of the alisphenoid and prootic, which is largely inclosed by the prootic, the alisphenoid forming only the anterior boundary. In assigning a similarly placed foramen to the third nerve in a skull of *Hypsilophodon*, Hulke[a] appears to be in error.

The determinations of the foramina of this region differ somewhat from those of Andrews[b] for the skull of *Iguanodon*, due to the different arrangement of the foramina entering the foramen lacerum posterius, *Iguanodon* having both an anterior and posterior branch instead of being single as in *Camptosaurus*.

The pituitary fossa is deep, extending considerably below the floor of the median vesicle. Its ventral posterior angles mark the positions where the internal carotids enter the cavity diagonally from deep external fissures on the sides of the basisphenoid shown at *c*, fig. 5.

None of the skulls studied show the relations of the foramina anterior to those for the branches of the trigeminal or fifth nerve.

It is unfortunate that there is not a brain case sufficiently complete from which a cast of the brain cavity might be made, for it would show at once the great similarity to the brain of *Iguanodon* as described by Dr. C. W. Andrews. The ventral surface of the supraoccipital of Cat. No. 5473, U.S.N.M., if cast would show the same compressed cerebellum rising high above the hemispheres. This high dorsal development of the brain appears to be peculiar to *Camptosaurus* and *Iguanodon*, although there is a suggestion of it in the brain casts of some of the trachodont reptiles.

THE LOWER JAW.

A complete jaw of *Camptosaurus* is unknown, but a study of well preserved parts, representing several individuals which supplement one another, shows that each ramus is formed of seven separate bones, the two rami being joined anteriorly by a predentary. The arrangement of the bones of the posterior half of the ramus are admirably shown in No. 1887, Yale Museum (see Plates 8 and 9), and the description of this region is based principally upon a study of this specimen.

The dentary.—The dentary which forms the anterior half of the jaw is the largest of the elements composing it and bears along the outer part of its dorsal border aveoli for 15 teeth—on the inside 16 can be counted (see 2, fig. 8). Anteriorly it is somewhat com-

[a] Quart. Journ. Geol. Soc. London, XXXVI, 1880, p. 435.

[b] Annals and Magazine Natural History, 6th ser., XIX, p. 590.

pressed transversely with a part on the lower border of the anterior end, which curves in and was united with the dentary of the opposite side by cartilage only (see *ss*, fig. 8). Hulke's description of the anterior part of the mandible of *Hypsilophodon* as having a "spout-like symphysial end" aptly describes this region in *Camptosaurus*. Posterior to the symphysial surface the dentary swells somewhat transversely, but remains about the same depth throughout the dentigerous part, the upper and lower borders being nearly parallel. The lower border is almost straight, as shown in fig. 8. A short, blunt process rises from the dorsal surface just posterior to the last

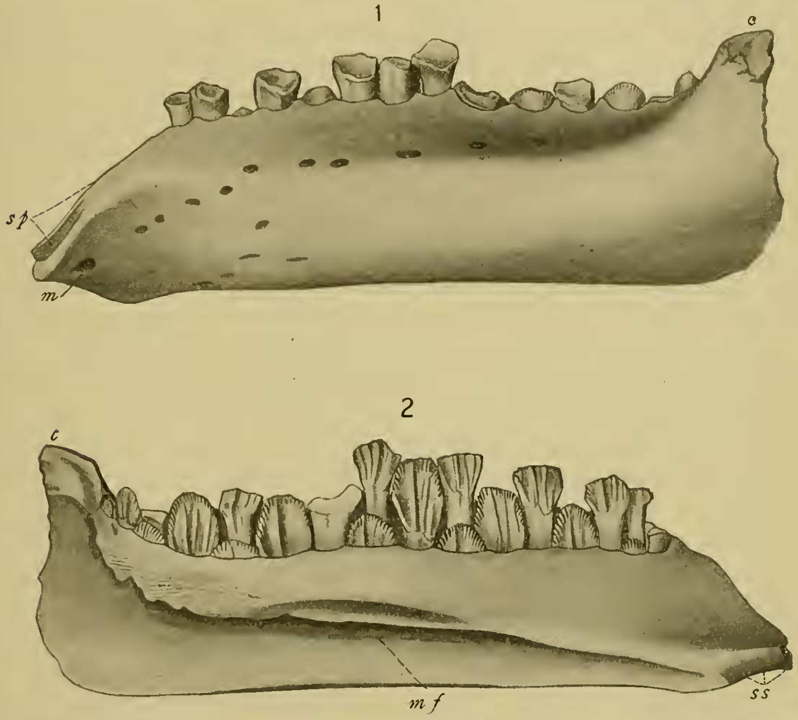


FIG. 8.—(1) EXTERNAL VIEW OF LEFT DENTARY, CAMPTOSAURUS. NO. 1886, YALE MUSEUM, ½ NAT. SIZE. *c*, CORONOID PROCESS; *m*, MENTAL FORAMEN; *sp*. SURFACE FOR PREDENTARY. (2) INTERNAL VIEW OF SAME. *c*, CORONOID PROCESS; *mf*, MANDIBULAR FORAMEN; *ss*, SYMPHYSIAL SURFACE.

tooth and gives support on the internal side to the coronoid (see *c*, fig. 8).

Just beneath the base of the coronoid process there is a deep cavity (*mf*., 2, fig. 8) opening on the infero-internal surface of the dentary and extending forward nearly its entire length. This mandibular fossa is present in most reptilian jaws, and in *Camptosaurus* is inclosed principally by the overlapping splenial. Posteriorly the dentary is in contact with the angular, surangular, and prearticular. The dentary unites with the predentary by an oblique surface on the anterior end, commencing dorsally just anterior to the aveoli of the most anterior tooth, and terminating ventrally in a point above the lower border of the dentary. A concave ventral surface posterior to the anterior point or projection on the inward extension of the dentary, for cartilaginous union with its fellow of the opposite side, apparently represents a surface for the reception of a posterior branch of the predentary after that found in *Stegosaurus* and *Triceratops*.

On the outer side of the dentary, about 20 mm. below the superior border, there is a series of foramina that extends the length of the bone. These doubtless served for the transmission of nerves and nutrient blood vessels to the lips.

The largest foramen on the external surface near the lower anterior end of the dentary at *m*, 1, fig. 8, probably represents the mental foramen through which a branch of the fifth nerve emerges.

The more important characters of the dentary of *Camptosaurus* are well shown in fig. 8, drawn from the left dentary of No. 1886, Yale Museum.

Surangular.—Externally the surangular meets the dentary and coronoid (?) just posterior to the coronoid process by a nearly vertical suture, and forms the upper border of the jaw, extending backward and downward to its posterior extremity. Ventrally it unites for its full length with the superior border of the angular. Its upper posterior surface is excavated and forms the external part of the cotylus for the articulation of the quadrate. There is a pronounced external mandibular foramen (see *sf*, fig. 2) on the outer median surface just posterior to its union with the dentary, as in *Triceratops prorsus* and *Iguanodon bernissartensis*.

Angular.—The angular forms the lower portion of the posterior third of the ramus, being wider in front than posteriorly. On the external surface, anteriorly, it is overlapped by a broad, thin, posterior finger-like prolongation of the dentary, as shown in figs. 1 and 2, Plate 8. Dorsally it meets the surangular and prearticular, and in conjunction with these elements, inclosed and held in position the small, block-like articular. On the anterior internal side it is overlapped by a posterior prolongation of the splenial. (See Plate 9.)

Articular.—The articular is a block-like bone higher than wide, and, as in many reptiles, when in position was probably the most posterior element of the mandible. In No. 1887, Yale University Museum, as shown by fig. 1, Plate 9, the articular has been crowded up and forward from its normal position in the jaw. It could not be determined whether there was an anterior prolongation of this bone lying between the prearticular and supra-angular, as this region is still enveloped in a hard sandstone matrix.

Prearticular.—In specimen No. 1887, Yale Museum, there was found to be an extra element on the postero-internal side of the ramus, which, from its position, I have identified as the prearticular. Marsh considered this bone the articular, as is indicated by the abbreviation "art." still remaining on the specimen and plainly shown in fig. 1, Plate 9, reproduced here from a photograph. This interpretation, however, leaves the small element on the supero-posterior part of the jaw without designation. That these two bones are distinct elements there can be no question, as all of the sutures in this specimen are clearly defined, and, moreover, the posterior part of the ramus of No. 1880, Yale Museum, shows the articular in position while the prearticular has been displaced and is missing.

Dollo[a] considers an element occupying a similar position in the jaw of *Iguanodon bernissartensis* the surangular. I am inclined to believe that this element represents the prearticular and that the surangular is on the supero-external part of the posterior end of the ramus, as in *Camptosaurus*, but which he indicates as the articular. The presence of an external mandibular foramen occupying relatively the same position as found in the surangular of *Camptosaurus* (see fig. 2, *sf*) is also suggestive of the correctness of this interpretation.

In *Camptosaurus* the prearticular is an elongate bone lying dorsal to the supero-internal border of the angular, and extending nearly if not fully to the posterior termination of the jaw. Anteriorly its forward extremity is covered by the overlying splenial. Its upper posterior border is concave and, with the surangular and articular, forms a cotyloid surface for the quadrate. In comparison with the size of the end of the quadrate this surface is capacious, an arrangement which would have permitted of free movement of the jaws upon the quadrate. On the internal median surface, just before this element disappears under the splenial, may be seen an elongated oval foramen, which probably represents the internal mandibular foramen of most reptiles (see *f*, Plate 9, fig. 2). I do not know that this element has been observed before in a member of the orthopodous dinosaurs, although it is present in most turtles and members of the Pelycosauria, and it would appear to indicate a primitive arrangement of the elements of the mandible.[b]

Splenial.—The splenial is a comparatively thin, flattened bone applied to the inner surface of the ramus. On the lower posterior

[a] Dollo, Bull. Bruxelles Mus. Roy. d'Hist. Nat. de Belgique, II, 1883, pl. IX, fig. 3.

[b] Williston gives an interesting discussion of this element in his description of *Dolichorhynchops* (Field Columbian Mus. Pub. No. 73, Geol. Ser., II, No. 1, 1903, pp. 29 to 32). He calls attention to the fact that Baur (Amer. Nat., 1891) believes that the element usually considered the articular is composed of two bones in the young *Sphenodon* and the conditions found in the jaws similar to those of the Testudinata. Baur assumes these elements to be present in all reptilian mandibles, but in the adult skull their identity becomes obliterated by the ankylosis of the suture.

border it sends back a thin, finger-like process which laps along the anterior internal surfaces of the angular and prearticular. From an examination of mutilated specimens it appears there was a long tapering anterior process which covered over the mandibular fossa in the dentary, and extended nearly to the anterior symphysisal end. It met the coronoid by a horizontal suture below the level of the functional teeth (see fig. 2, Plate 9). The median ventral border is swollen transversely and extends below the dentary and angular, and is visible from a lateral view of the mandible.

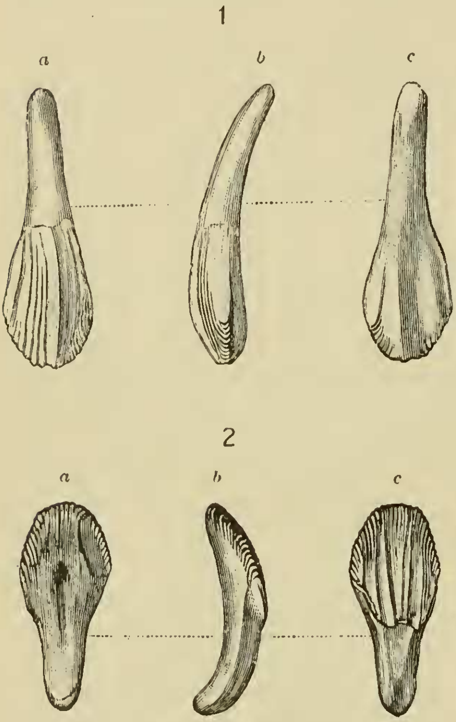


Fig. 9.—(1) Tenth upper tooth; (2) fifth lower tooth of Camptosaurus medius Marsh. No. 1880, Yale Museum. Holotype. Nat. size. *a*, outer view; *b*, view of posterior border; *c*, inner view. After Marsh.

Coronoid.—The coronoid is a small, flattened bone roughly triangular in outline. It unites ventrally with the splenial, dentary, and surangular, and the lower external surface laps along the internal surface of the short dorsal process of the dentary, extending above it and terminating in a compressed, rounded end. Its general outline is shown at *co.*, fig. 2, Plate 9.

Predentary.—The predentary is unknown, but after a comparison of camptosaurian remains with those of allied forms, I am inclined to the opinion that when found it will be more after the pattern of *Iguanodon* than of *Triceratops*, as Marsh has indicated it in the first restoration of the mandible. In the restoration of the skull (see fig. 2), the predentary as drawn is a modification of that of *Iguanodon.*

The teeth.—The teeth of both upper and lower jaws when unworn are spatulate with serrated margins. A representative tooth selected for description from the maxilla measures 38 mm. in length, of which 19 mm. belong to the crown. The root is cylindrical, gradually tapering from the base of the crown to its end. As shown by broken teeth, there was a large pulp cavity extending well up into the crown. The outer surface of the upper and the inner surface of the lower teeth are sculptured by longitudinal ridges passing from the union of the crown and root to the upper border of the former. Every tooth shows one pronounced longitudinal ridge, which is always, whether it be upper or lower, posterior to the median line, having on each side a varying number of secondary ridges (fig. 9). There are more of the secondary anterior to the main ridge than there are posterior. The secondary ridges are also more numerous and stronger in teeth of the upper than in those of the lower jaw, a character which serves to distinguish detached teeth. Many of these ridges subside before reaching the base of the crown; none are serrated as is the case in the teeth of *Iguanodon*. The teeth at either end of the dental series, whether it be upper or lower, are slightly smaller than those intermediate. The contour of the larger teeth appears to be less angular than the smaller. Both upper and lower teeth are curved longitudinally, this curvature inclining the crowns of the upper teeth inward to meet those of the lower jaw, which are similarly inclined outward. Nearly all crowns which project fully above the level of the outer border of the alveolar process show marks of wear, being obliquely ground. The ridged surface, having thick enamel, stands longer and forms a cutting edge, which at first is serrated, but later becomes sinuous as the longitudinal ridges become cross sectioned. The inner surfaces of the crowns are smooth, gently convex antero-posteriorly, and unsculptured, the terminal marginal serration showing slightly upon it. When much worn these spatulate teeth are reduced to flattened stumps, as shown in the figures. Hulke[a] says of the teeth of *Hypsilophodon:* "By the time the crown is worn to the level of the aveolar border of the jaw, the tapering cylindroid root has been absorbed, so that a very slight force would suffice to detach the remnant in this condition." In *Camptosaurus*, however, they appear to be forced out before the absorption of the root, as will be seen by an examination of figs. 8 and 10.

FIG. 10.—INTERNAL VIEW OF RIGHT DENTARY, CAMPTOSAURUS DISPAR? MARSH. CAT. NO. 5819, U.S.N.M. ½ NAT. SIZE. *a*, ANTERIOR END; *b*, DENTARY; *p*, POSTERIOR END.

The arrangement of the teeth in a longitudinal and vertical series is well shown in figs. 8 and 10. Successional teeth in the dentary are seen below and between those of the functional row. In the maxillæ these teeth descend as usual on the inner side of those in use. Thus, in the upper jaw they replace on the unsculptured and in the lower

[a] Phil. Trans. Roy. Soc. London, CLXXIII, 1882, p. 1042.

on the sculptured sides of the functional teeth. There appears to be only two teeth in a single vertical series. In the dentary of Cat. No. 5819, U.S.N.M. (see fig. 10), four phases of the successional teeth are shown, (1) stumps about to be shed, (2) teeth whose crowns are in full wear, (3) germ crowns which have only partly emerged and not yet in use, (4) tips of germ crowns just appearing above the inner parapet.

The dentary, as shown by several individuals, bears from 14 to 16 teeth, and the maxillary probably an equal number. As shown in figs. 8 and 10, the teeth appear to rise as two or more oblique rows, those posterior being the higher in each row. None of the jaws studied show the regular arrangement of the teeth found in *Iguanodon*, as figured by Dollo.[a]

All of the maxillæ and dentaries examined show a great irregularity of the functional row as exhibited in figs. 7, 8, and 10.

Nicholson and Lydekker[b] were the first to point out that the teeth of *Camptosaurus* "were somewhat similar in their structure to those of *Iguanodon*," but by most authorities they are considered simpler in their sculpturing.

Hyoid.—That there is a well-developed hyoid in *Camptosaurus* is shown by specimen No. 1887, Yale Museum (see *h*, fig. 2, Plate 9), which has the thyrohyal of the left side preserved nearly *in situ*. It is an irregularly rounded curved bar with a slightly expanded, rounded, anterior extremity. Posteriorly it gradually tapers to a small, smooth, round end. Marsh[c] has called attention to the resemblance of this element to the hyoid in *Iguanodon*.

The principal measurements of this element of a very large individual are as follows:

	mm.
Greatest length	152
Greatest width of anterior end	18
Greatest width of posterior end	7

THE VERTEBRAL COLUMN.

As nearly as can be determined, the vertebral formula of *Camptosaurus* is as follows: Cervicals, 9; dorsals, 16?; sacrals, 4 or 5; caudals, 44+. There are no true lumbars.

In giving the formula as above, the cervicals may be considered absolutely determined, as shown by complete necks in four different individuals. Specimens Cat. Nos. 4282 and 2210, U.S.N.M., agree in having 16 dorsals, the most posterior of which is modified to give some support to the first sacral rib, and should properly be considered a sacro-dorsal. I have considered as sacrals

[a] Bull. Bruxelles Mus. Roy. d'Hist. Nat. de Belgique, II, 1883, pl. IX, fig. 3.

[b] Manual of Paleontology, p. 1159.

[c] Amer. Journ. Sci., XLVII, 1894, p. 246.

only those vertebræ which support sacral ribs, and this interpretation does not include all of those sutured by their centra in adult individuals, as will be discussed later. In the two specimens referred to above, there are preserved 33 and 34 caudals respectively, and I have estimated that probably nine or more would be required to complete the series. In regard to the caudal series in *Camptosaurus*, it appears to agree approximately with the number found in complete specimens of *Iguanodon*, which varies from 46 to 48.

The atlas.—The atlas is composed of four separate pieces, the intercentrum, two neural arches or neuracentra, and the odontoid process. The intercentrum is a subcrescentic block of bone, the longer axis being transverse. Viewed from above, the median surface is concave, forming a hollow in which the anterior rounded portion of the odontoid rests. The anterior part of this concave surface is more deeply excavated, forming a shallow, transverse groove in which a corresponding ridge on the antero-inferior surface of the odontoid fits. On either side of the median depression are the articular faces which look upward and outward, and on which the pedicles of the neuracentra rest. The posterior view presents a nearly vertical face, rounded only on the median inferior border. Inferiorly and on either side are well developed facets for the articulation of the cervical ribs of the atlas. The anterior face superiorly is deeply excavated, forming the lower portion of the cup for the reception of the occipital condyle, the anterior border being lip-like where it underlaps the articular surface of the condyle.

None of the specimens studied has the upper expanded ends of the neuracentra complete. The articular end is about evenly divided into two faces which meet at an obtuse angle. The posterior face rests upon the intercentrum, while the other looks forward and downward and forms part of the cup for the occipital condyle. Above the articular end just described, the shaft is constricted, but superior to this neck it widens again, but as to its further extent the available material shows this part to be lacking. As in other dinosaurs, the neuracentra articulate posteriorly with the anterior zygapopyses of the axis.

The *odontoid* is slightly cupped posteriorly, and though closely applied to the axis, shows no indication of coalescence in any of the specimens studied. The upper surface forms the floor of the neural canal and is slightly concave transversely. The anterior half of the odontoid is slightly constricted, forming a short neck (see 1, fig. 11). Inferiorly the surface is rounded, the posterior half having a smooth, transversely rounded articular surface which is in contact with the upper concave surface of the intercentrum. The smooth anterior end is rounded both vertically and horizontally where it abuts against the posterior end of the occipital condyle. In passing, it may be of interest to note that the atlas of *Stegosaurus* is, in nearly all respects, very similar.

Measurements of atlas, Specimen Cat. No. 5473, U.S.N.M.

	mm.
Greatest length of intercentrum antero-posteriorly	23
Greatest width of intercentrum	58

The axis.—The axis of specimen Cat. No. 5473, U.S.N.M., as preserved is fairly complete, and it is upon this that the following detailed description is based, although many of the facts are supplied from the incomplete axes of Cat. Nos. 2210 and 5474, U.S.N.M., and 1877, the holotype of *C. dispar*, in the Yale University Museum.

The centrum is plano-concave, the cup being moderately deep. Medially the centrum is constricted both laterally and inferiorly but without ventral keel. The anterior extremity is more expanded laterally than the posterior, the width of the former exceeding the total length, as shown in fig. 12. On the lateral median surfaces are two small vascular foramina. These are not present, however, in the axis of Cat. No. 5474, U.S.N.M., but are represented by shallow cavities or depressions.

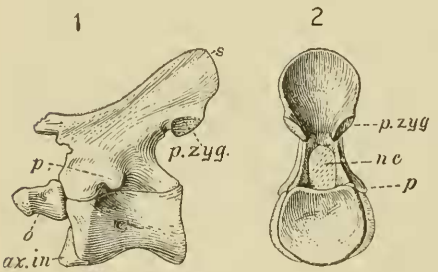


Fig. 11.—(1) Axis and portion of atlas of Camptosaurus dispar Marsh. Cat. No. 5473, U.S.N.M., side view, ¼ nat. size; (2) posterior view of same; *ax. in*, second intercentrum; *nc*, neural canal; *o*, odontoid; *p*, diapophyses; *p. zyg*, postzygapophyses; *s*, neural spine.

The neural arch is composed of two parallel plates of bone, which, as they rise from the centrum, gradually converge, uniting above and forming a sharp median longitudinal crest. Transversely the neural spine is compressed, but it extends out over the centrum at either end, more especially the posterior (see fig. 11). This portion of the spinous process rises somewhat and flares out into a comparatively thin frill-like plate which overhangs the centrum of the succeeding vertebra. Posterior zygapophyses, which look downward and outward, are well developed on the lower borders of the overhanging part. The anterior prolongation of the spinous process is hardly more than an anterior development of the median crest. Although it appears that the anterior zygapophyses were probably present, this part of the bone in all of the specimens studied is damaged, and their shape and position could not be determined.

A weak diapophysial process which extends outward and downward (see *p*, fig. 11), is developed on the median, infero-lateral surface of the pedicle of the arch. Viewed posteriorly the neural canal is subelliptical in outline, the longer axis being vertical.

The most striking feature of the axis is the presence of a second intercentrum firmly co-ossified with the inferior surface of the anterior extremity of the centrum. Attention has been called to this element in a former paper [a] as follows:

In comparing the axis of *Morosaurus agilis* with the homologous parts of other Dinosaurian specimens in the U. S. National Museum, the writer found, on the axes of two individuals of the genus *Camptosaurus*, intercentra attached by suture to the centra of the axes. So far as the writer is aware, this element has not been observed before in a representative of the Orthopoda. In the smaller (No. 5474, U.S.N.M.) and probably younger specimen the intercentrum has been somewhat crushed out of position, but in the larger specimen (No. 5473, U.S.N.M.) it is retained in place. * * *.

Inferiorly the intercentrum of *Camptosaurus* is roughly subelliptical in form, the longer axis being tranverse. It is closely united by suture to the lower half of the anterior end of the centrum, forming a prominent lip-like projection which, when articulated, underlaps somewhat the centrum of the atlas [see fig. 12]. In a fully adult specimen this element would probably become coossified, as in *Morosaurus grandis*, and thus lose its identity. Viewed from the side, it is triangular in form, the deepest portion being next to the centrum. The inferior surface is gently convex transversely and slightly concave antero-posteriorly. Seen from the front, the center has the greatest vertical depth, the upper margins gradually sloping down to the lateral borders. The anterior face is smooth and somewhat concave supero-inferiorly. There are two small pits on the median anterior part of the inferior surface. The presence of an axis intercentrum in both the Opisthocoelia (Sauropoda) and Orthopoda (Predentata) tends to confirm somewhat the contention of Marsh and Hatcher that the Dinosauria is a natural group, and in the examples cited here it should be considered a persistent primitive character which was present in a remote but common ancestor.

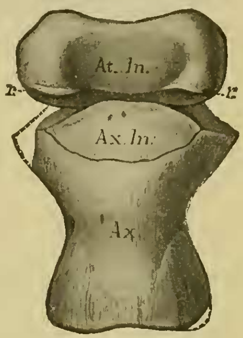


FIG. 12.—VENTRAL VIEW OF ATLAS AND AXIS OF CAMPTOSAURUS DISPAR MARSH. CAT. NO. 5473, U.S.N.M.; $\frac{1}{2}$ NAT. SIZE. *at. in*, ATLAS INTERCENTRUM; *ax*, AXIS; *ax. in*, SECOND INTERCENTRUM; *r*, FACETS FOR RIB.

The second intercentrum is also present in the typical skeleton of *Camptosaurus nanus*, although not suturally united.

In 1889 Lydekker [b] called attention to the axis of a dinosaur from the Wealden of the Isle of Wight, which had an axil intercentrum attached to it. After comparing it with Marsh's figures of the axis of *Ceratosaurus nasicornis* (holotype, Cat. No. 4735, U.S.N.M.), he considers the general resemblance so close as to indicate the probability of its belonging to the same suborder. He says: "It therefore seems highly likely that it may be referable to the Wealden species of *Megalosaurus* or to a nearly allied form."

[a] C. W. Gilmore, Proc. U. S. Nat. Mus., XXXII, 1907, p. 164.

[b] Quart. Journ. Geol. Soc. London, XLV, 1889, pp. 44, 45.

After a comparison of Lydekker's figures of this specimen (see fig. 13) with the axis of *Camptosaurus*, and noting the many similarities in proportion and position of the processes, together with the presence of an intercentrum on both and the absence of a ventral keel on the centrum of the British specimen, so plainly shown on the axis of

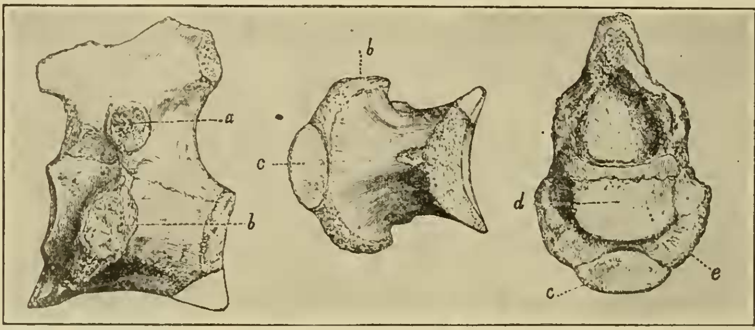


Fig. 13.—Left lateral, ventral, and anterior aspects of the axis of an Orthopodus? dinosaur from the Wealden of the Isle of Wight No. R. 1412 British Museum. ½ nat. size. *a*, diapophyses; *b*, parapophyses; *c*, second intercentrum; *d*, articulation for odontoid process; *e*, articulation for intercentrum of atlas. After Lydekker.

Ceratosaurus, I am quite convinced that this axis pertains to one of the orthopodous dinosaurs rather than to one of the carnivorous forms. It might possibly be referred to *Camptosaurus ? valdensis* Lydekker, also from the Wealden of the Isle of Wight.

Measurements of Specimen, Cat. No. 5473, U.S.N.M.

	mm.
Greatest length of centrum of axis	55
Greatest width anterior extremity	59
Greatest width posterior extremity	45

The third cervical.—The third cervical may be distinguished by its plano-concave (platycœlian) centrum and by the fact that if the planes of the articular surfaces were produced ventrally they would intersect within a foot below the ventral surface of the centrum (see Plate 12). In the succeeding cervicals just the opposite condition is found, that is, the produced planes of their articular ends would meet dorsally. In the articulated cervicals the upward curve of the posterior cervicals changes with the third vertebra to a forward and downward direction, thus giving the neck a graceful sigmoid curve very bird-like in character.

The lateral surface of the centrum is constricted transversely, but flares out posteriorly. The centrum is more regularly rounded, the sides being convex vertically, and it lacks the decided ventral keel found in the cervicals which follow.

There is a well-developed capitular process on the side of the centrum near the anterior end just below the neuro-central suture, and a weak tubercular process near the middle lateral surface of the neural process, posterior and below the level of the prezygapophyses. As in the axis the neural canal is large, being higher than wide, with thin walls.

The postzygapophyses are a pair of slender, divergent processes which extend upward, backward, and outward, their articular faces looking downward and outward. A low, median crest of bone rises posterior to the bases of the prezygapophyses and extends posteriorly to the dividing point of the branches of the zygapophyses.

Cervicals posterior to the third.—Marsh has observed:[a] "The cervical vertebræ are all opisthocœlous." In this he was evidently mistaken, as is clearly shown by a study of several individuals which have the complete cervical region preserved. The axis and third cervical are always platycœlian. In most individuals, however, the remaining cervical centra are opisthocœlian, though more strongly so in the posterior than in the anterior cervicals. In Cat. No 5474, U.S.N.M., the cervical centra, comparatively speaking, remain quite plane throughout the series.

Viewed from the anterior end, the centra are shield-shaped (see 2, fig. 14). Below the neuro-central suture the sides are deeply pinched in, forming lateral depressions which are deeper toward the front, and concave in the longitudinal direction, the articular ends being expanded. Ventrally there is a strong angular keel which widens at either end, more especially the posterior. The ventral surfaces of the ends are roughened by coarse, irregular, longitudinal striæ. All of the cervicals have capitular facets on the sides near the anterior end (see *p*, fig. 14). In the anterior region the facets are just below the neuro-central sutures, but in the posterior cervicals, beginning on the fifth in Cat. No. 5473, U.S.N.M., the suture bisects the facets, and thus both the centrum and the neural arch contribute to their formation.

The neurapophyses in all of the cervicals have an extensive attachment to the centrum, spreading out conspicuously at the ends, more especially the anterior, as shown in fig. 14.

Well-developed diapophyses extend outward from the sides of the neura- and prezygapophyses, shown at *d*, fig. 14. These gradually increase in length from the third to the ninth. The tubercular facets on their outer extremities look downward and outward. The neural canal remains large throughout the neck, becoming nearly circular in the posterior members. The prezygapophyses are wide apart, their articular faces looking inward and upward. Neural spines are not

[a] Amer. Journ. Sci., XVIII, Dec., 1879, p. 501.

present in the cervicals of *Camptosaurus* unless the weak, median, crest-like ridge found on the posterior elements might be interpreted as such. Dorsally the neural arch consists of a broad, transversely rounded surface which extends backward and upward, the posterior termination giving off the divergent branches of the postzygapophyses. The height of the arch gradually increases posteriorly. Posteriorly just below the junction of the posterior zygapophyses is a pit-like foramen leading forward into the neural process. While this foramen is present in all of the cervicals pertaining to Cat. Nos. 4282 and 5474, U.S.N.M., and in the type of *C. dispar*, No. 1877, Yale Museum, they are entirely lacking in the cervical region of Cat. No. 5473, U.S.N.M.

Fig. 14 (1 and 2) shows the side and front views of the eighth cervical of Cat. No. 4282, U.S.N.M., which may be considered typical of the vertebræ of the posterior part of the neck.

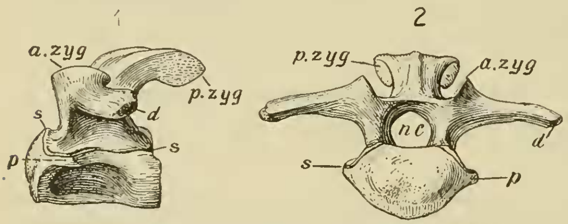


Fig. 14.—(1) Eighth cervical vertebra of Camptosaurus browni. Holotype. Cat. No. 4282, U.S.N.M.; ¼ nat. size, side view; (2) anterior view of same; *a zyg*. prezygapophyses; *d*, diapophyses; *nc*, neural canal; *p*, parapophyses; *p. zyg*, postzygapophyses; *s*, neuro-central suture.

Marsh has given the united length of the nine cervical vertebræ in the holotype of *C. dispar* as 565 mm. The complete cervical region of No. 5473 (see Plate 12) measures 590 mm. and No. 5474, 440 mm. The principal measurements of the cervicals of *Camptosaurus* will be found in table on pages 242 and 243.

Dorsal vertebræ.—As mentioned previously, there are 16 dorsals present in the vertebral series of both Cat. Nos. 4282 and 2210, U.S.N.M. It is true, as found, there were interruptions in the series, i. e., not all were found articulated, but after a critical study of the two columns it appears quite probable that 16 will be found to be the correct number. It can not be stated definitely from the known material, but the evidence, at least, points very strongly to the shortening of the presacral series by at least five vertebræ from the number given this animal by Professor Marsh in his restoration of *Camptosaurus dispar*. (See Plate 18.)

The first dorsal.—In specimen Cat. No. 4282, U.S.N.M., the first dorsal was, fortunately, found interlocked by its zygapophyses with the last cervical. As mentioned previously, the first dorsal, and cervicals seven, eight, and nine, were taken up in a single block of matrix (see Plate 6, original field numbers 76, 83, 78, and 77), and reached the laboratory occupying their original relative positions. In consideration of these facts, there can be no question regarding the association of these vertebræ.

That the vertebra now under consideration was a dorsal is shown by the sudden change of the capitular facet from the anterior lateral surface of the centrum on cervical nine, to a point well up on the side of the arch beneath the transversely extended process or diapophysis, and by the great development of the transverse process. The capitular facet is also well developed as compared with the weak facets of the cervicals anterior to it. This facet is slightly cupped and subcircular in outline, being somewhat elongated in the vertical axis.

The length of the centrum of No. 4282 is slightly less than in the preceding vertebra. There is a pronounced cup on the posterior end of the centrum, but anteriorly the end is less convex than in the cervicals preceding, and, as Marsh has pointed out in his description of the cervical region of *Ceratosaurus*, could only be inserted a short distance into the adjoining cup. This distance is accurately marked on the centrum by a narrow, articular border, just posterior and external to the median flattened anterior face. While there are no lateral cavities in this centrum, the sides are deeply excavated, both laterally and inferiorly. The inferior surface presents a narrow, median, longitudinal ridge which widens at either end, more especially the anterior. The surface of this anterior expansion is roughened with longitudinal striæ.

The neural arch is high and incloses a large, circular neural canal. The expanded pedicles of the arch are firmly attached to the centrum by suture. Antero-posteriorly the arch, above its base, is considerably shorter than the centrum, the diapophyses rising from the sides of the arch and extending upward and outward at an angle of 45°, as stout, subtriangular processes. The terminations of the diapophyses are lacking in all available specimens. The anterior zygapophyses look decidedly inward and slightly upward, and are elliptical in outline, with the greatest diameter antero-posteriorly. Connecting the anterior zygapophyses at their inferior margins is a thick, rounded shelf of bone which forms the covering of the anterior portion of the neural canal. From the middle, and somewhat posterior to the anterior border of this shelf, a low spinous process is developed, which, in No. 1877, Yale Museum, has a height of 11 mm. Superiorly its termination is angularly rounded antero-posteriorly and slightly thickened transversely. This spine is missing in all of the other specimens studied. Posterior to the anterior zygapophyses and lateral to the median spine are deep depressions in the top of the process. The postzygapophyses are missing on the first dorsal of No. 4282, but are present on that of *C. nanus*, No. 2210. They extend far back beyond the posterior end of the centrum, their articular faces looking outward and downward. From a posterior view, both vertebræ show, just above the neural canal, a median pit which extends forward and downward into the arch.

The second dorsal.—This vertebra differs from the preceding chiefly by the development of a higher spinous process, more robust transverse processes, greater length of centrum, and more elevated position of the capitular facets on the lateral surface of the neurapophyses. The distal extremity of the centrum is not so deeply cupped as in the preceding vertebra, and the anterior extremity is nearly plane, being only slightly concave dorso-ventrally. In median cross section the centrum would be wedge-shaped. The subcircular neural canal is more reduced, and the tubercular rib facet looks downward and forward.

The third dorsal.—The third dorsal (see fig. 15) may be distinguished from the second by the increased size of the tubercular and

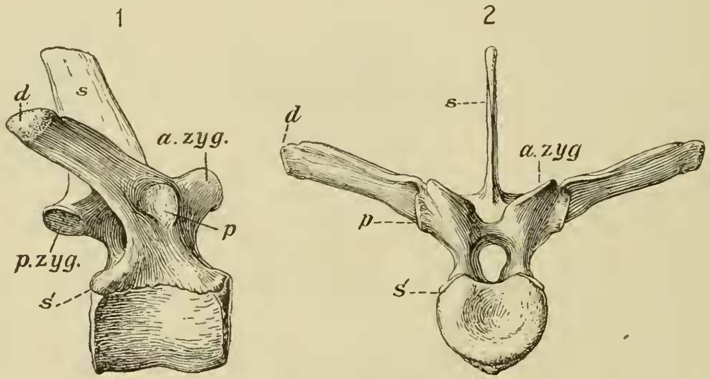


FIG. 15.—(1) THIRD DORSAL VERTEBRA OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE, SIDE VIEW; (2) ANTERIOR VIEW OF SAME; *a. zyg*, PREZYGAPOPHYSES; *d*, DIAPOPHYSES; *p*, PARAPOPHYSES; *p. zyg*, POSTZYGAPOPHYSES; *s*, NEURAL SPINE; *s'*, NEURO-CENTRAL SUTURE.

capitular facets, and the more elevated position of the latter. Also by the more rounded ventral surface of the centrum, which slightly exceeds the second in length.

Dorsals four to fourteen.—The succeeding vertebræ are so similar in most respects that they may best be described together. The centra, allowing for distortion by crushing, gradually increase in length from the first to the twelfth, which is the longest of the series in No. 4282. They have their articular extremities concave, more especially on the posterior end, but to a less degree than in those vertebræ anterior. The depressions so marked in the sides of the cervical and anterior dorsal regions below the neuro-central suture, decrease in approaching the trunk, and from the fourth dorsal to the loins the sides are approximately flat vertically, though concave longitudinally, caused by the expansion of the ends of the centra. There is also a diminished angularity of the keel so that the vertebræ of the mid-dorsal region have rounded ventral surfaces. Posteriorly the centra gradually increase in bulk.

The elevated neural processes of the anterior dorsal region become lower posteriorly, while the low, thin, plate-like neural spines gradually increase in height, with thickened terminal extremities that reach their maximum development in the sacral region.

The transverse processes, stout and relatively long in the anterior dorsal region, have a capitular facet on the fourth dorsal, well up under their front edges, where they spring from the neural arch, and tubercular facets on their outward extremities (see *d* and *p*, fig. 15). The capitular facet withdrawn from the centrum on the first dorsal reaches the anterior border of the diapophysis in the fourth. Posteriorly the capitular facet gradually moves outward on the anterior

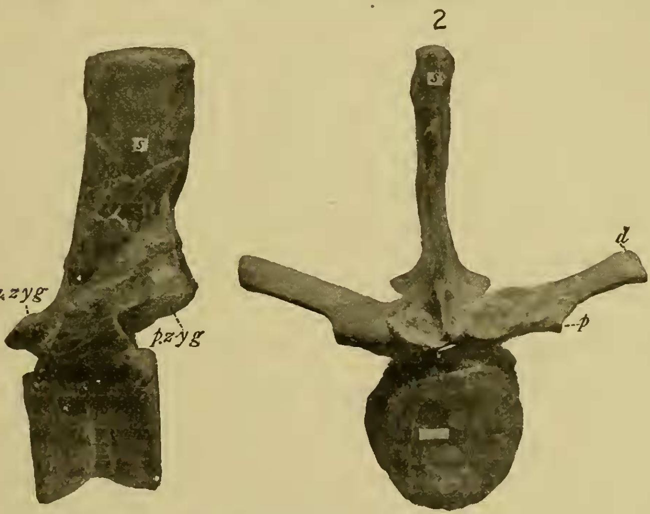


FIG. 16.—(1) THIRTEENTH DORSAL VERTEBRA OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ⅓ NAT. SIZE, SIDE VIEW; (2) ANTERIOR VIEW OF SAME; *a. zyg.* PREZYGAPOPHYSES; *d*, DIAPOPHYSIS; *p*, PARAPOPHYSIS; *p. zyg*, POSTZYGAPOPHYSIS; *s*, NEURAL SPINE. FROM A PHOTOGRAPH.

face of the transverse. Judging from the size of the capitular facet and the capitulum of the rib preserved in place, the seventh dorsal supports the heaviest rib of the series in No. 4282. The transverse processes are directed backward and somewhat upward from the horizontal as they leave the neural arches, and from the mid-dorsal region posteriorly they become more slender and somewhat shorter, with a decrease in size of the tubercular and capitular facets (see fig. 16, *d* and *p*). The diapophyses of the dorsals are supported by heavy buttresses or lamina which rise obliquely forward to their under surfaces from the lower and back part of the neurapophyses. They form the outer boundary of deep, three-sided hollows, as shown in fig. 15. These cavities gradually grow shallower from front to back. The posterior zygapophyses overhang the end of the centrum, this character being especially pronounced in the posterior dorsal region (see fig. 16). The neural canal remains about the same size from the fourth to the fourteenth.

The fifteenth dorsal.—This vertebra may be at once distinguished by its short centrum (see dorsal No. 15, table of measurements, page 243), which in No. 4282 is cylindrical in outline, with a weak ventral keel. The articular ends are concave, more especially the posterior. Antero-posteriorly it is the shortest of the dorsal series. The transverse process is short, wide, and directed outward at right angles to the neural process. It has weak tubercular and capitular rib-facets, which show that it carried a double-headed rib.

The sixteenth dorsal or sacro-dorsal.—The last dorsal centrum (sacro-dorsal) is longer and heavier than the one preceding and is the most robust of the vertebral series of No. 4282 (see *sd*, fig. 17). The two articular extremities are slightly concave, the posterior having a rough, rugose surface. Antero-posteriorly the sides are deeply concave, the inferior surface being pinched together, forming a short, pronounced median keel which expands transversely at either end. This vertebra in No. 1877*a*, paratype of *C. dispar* (Yale University Museum), is regularly rounded in this aspect and without ventral keel. On the supero-posterior angles are roughened, obliquely placed surfaces which give partial support to the first sacral ribs. The neuro-central suture is relatively shorter than in the preceding dorsals, a groove for the exit of a nerve limiting its extent posteriorly. The arch is higher than those immediately in front, and supports a weak diapophysis without parapophysial facet, indicating the presence of a single-headed rib which may have articulated with a small articular area on the internal side of the preacetabular process of the ilium. In No. 4282, the outer extremity of this process is missing, but it is plainly shown in the typical specimens of *C. dispar* and *C. nanus*, Plate 13 and fig. 39. As shown in fig. 17, the prezygapophyses are large and look almost directly upward. The spinous process is missing on this vertebra of No. 4282, but is present in No. 1877*a*, Yale Museum (see Plate 13). It is shown as a rectangular plate-like spine rising high above the diapophysis. The superior termination is thickened transversely, more especially on the anterior part of this border, which is heavier than the spine that follows, and, in this species (*C. dispar*), probably marks the maximum development of the spinous processes. The greatest height of this vertebra, taken at the center of the centrum, is 330 mm. The spine has a vertical groove on its posterior border extending nearly to its top. The postzygapophyses overhang considerably the end of the centrum.

The sacrum.—In specimen Cat. No. 4282, U.S.N.M., there are seven vertebræ united by a suture in the sacral region. Of this series I have considered as sacral only those vertebræ which support true sacral ribs. This interpretation excludes the anterior and posterior vertebræ, which may be regarded as sacro-dorsal and sacro-caudal, respectively, thus reducing the number of sacrals to five, as originally determined by Marsh for *C. dispar*.[a] Typically, there are five vertebræ joined by suture, but, as shown in Plate 13, *a*, the anterior one would be considered a dorsal. Hence in *C. dispar* there are only four true sacrals.

Sacrals two and three were found to be firmly coossified (see fig. 17, S_2 and S_3), and in this respect quite at variance with Professor Marsh's earlier determinations. In describing the type-specimen of *C. dispar*, he says:

> This genus agrees with *Laosaurus* in one important character, namely, the sacral vertebræ are not coossified. That this is not merely a character of immaturity is shown by some of the other vertebræ in the type-specimen, which have their neural arches so completely united to the centra that the suture is nearly or quite obliterated. To this character of the sacral vertebræ, the name of the present genus refers.

While the neural arches of the specimen here considered are attached to the centra throughout the column, the sutures in all instances are plainly discernible. Inasmuch as a second specimen in the National Museum, No. 4753, the holotype of *C. depressus*, has all of the vertebræ of the sacral region firmly coossified, it would appear that what Marsh considered a very important character of the genus, namely, the noncoalescence of the sacral vertebræ, can not be relied on as being a constant character. Moreover, the union of the other centra in the sacrum of specimen No. 4282 were very close and particularly strong, and it was with some difficulty that they were separated for the purpose of study. So firmly are sacrals two and three coossified that in places the suture is entirely obliterated (see fig. 17).

The first sacral may be distinguished by the great transverse expansion of the anterior end of the centrum. Both extremities have roughened sutural surfaces, which unite closely and strongly with the centra both preceding and following. The anterior face is somewhat angularly convex, while the posterior is slightly concave. The inferior surface lacks the decided keel of the last or sacro-dorsal and is more evenly rounded. The neural canal is much expanded, as shown in fig. 17, S_1. The posterior parts of the pedicles of the neural arch are very thin transversely and comparatively short anteroposteriorly, being to a limited extent borne on the last dorsal. The spinous process, as shown in Plate 13, is very similar to that of the last dorsal described above, but is more anteriorly placed in relation to the centrum. A long diapophysis extends out over the top of the first sacral rib, which, in some individuals, is firmly ankylosed to that bone. In No. 1877*a*, however, the suture remains distinct.

[a] Amer. Journ. Sci., XLVII, 1894, p. 246.

The centra of sacrals two and three are much compressed transversely, as shown in fig. 17, S_2 and S_3, the third being the smallest of the five. Antero-posteriorly the lateral and ventral surfaces are deeply concave. The inferior surface of sacral two is somewhat pinched together inferiorly, while sacral three is broader and flattened in this aspect.

The fourth sacral was firmly united to the fifth, although the suture is plainly seen. Like those preceding, the sides are concave antero-posteriorly, though the centrum as a whole is more robust than either sacrals two or three. Its ventral surface is somewhat flattened transversely, though concave longitudinally. Unfortunately only the centrum of the fifth sacral is preserved in this specimen. It differs but little from the fourth sacral, except that the rib or transverse process is not borne intervertebrally, as are those preceding, but is confined wholly to the anterior half of this centrum, which has a fragment of the articular end still attached, as will be seen by reference to fig. 17. The centrum is also more cylindroid in outline and the floor of the neural canal is much constricted transversely, as in the fourth of *C.* (*Iguanodon*) *prestwichii.* The latter observation is also true of the fourth or last sacral (fifth sacral of Marsh) in No. 1877*a*, Yale Museum, as is plainly shown in fig. 37, 3. A specimen referred to *C. nanus*, in the American Museum of Natural History, which has this region articulated, shows that the ribs or transverse processes of this vertebra reached and gave support to the ilia.

The fourth is the first sacral to show the peculiar peg-and-notch articulation (see fig. 17), considered by Marsh as characteristic of the sacral region of *Camptosaurus.* He says:[a]

> The vertebræ of the sacrum, especially the posterior four, are joined to each other by a peculiar peg-and-notch articulation. The floor of the neural canal of each vertebra is extended forward into a pointed process (somewhat like an odontoid process), which fits into a corresponding cavity of the centrum in front. This arrangement, while permitting some motion between the individual vertebræ, helps to hold them in place, thus compensating in a measure for absence of ankylosis.

This articulation may have been present between sacrals two and three before ankylosis took place, but this can not now be determined. It is, however, present between sacrals three and four, four and five, sacral five and caudal one, and there are also faint indications of the same method of articulation between caudals one and two, and two and three (see *p*, fig. 18).

In this connection it is of interest to know that an examination of the type-specimens of *Laosaurus consors* and *Dryosaurus altus* shows that both specimens exhibit the same peg-and-notch articulation of

[a]Amer. Journ. Sci., XLVII, 1894, p. 246.

the sacral centra, although they have been described as being without it.[a]

The five sacrals give support to five sacral ribs on each side. These ribs, excepting the fifth, are supported intervertebrally by rough sutural areas on their superior junctions, the main support being given by the posterior vertebra of each pair.

The neural processes are either missing or only represented by detached fragments in *C. browni*, but in order to make the description complete, these will be described from the holotype of *C. nanus*, Cat. No. 2210, U.S.N.M., which has the anterior three unusually well preserved (see fig. 39). As in *C. dispar*, there are only four true sacrals in *C. nanus*.

The neural arch in sacral one is somewhat higher than the last dorsal, with a much enlarged neural canal. In sacrals one, two, and three, the arches are contracted antero-posteriorly and expand outwardly into strong buttresses which, with the sutural surface on the centra, give support to the sacral ribs. This antero-posterior contraction of the pedicles leaves vertical, elongate cavities opening into the enlarged intervertebral chamber of the neural cavity for the exit of sacral nerves. The arches are united by heavy and closely fitting zygapophyses. The postzygapophyses are shifted well forward over the center of the centrum.

The neural spines are flattened plates which, as they rise above the arch, gradually expand antero-posteriorly, terminating in an end slightly thickened transversely. The spines remain about the same height throughout, all being inclined somewhat backward. In this specimen the spines are distinct and show no indication of fusion, as is indicated by Marsh's first restoration of this region in *C. dispar*.

The diapophyses of sacral one, in specimen No. 2210, are considerably modified from the thoracic type. They join with an outward development of the pedicle, forming a continuous vertical articular face or buttress, with which the upper portion of the sacral rib articulates. The first is the heaviest of the series, and this sacral rib was undoubtedly the chief support for the ilium. The diapophyses of sacrals two and three are developed in the same manner, although lighter in construction.

In the sacrum of Cat. No. 4282, U.S.N.M., sacral ribs one and two were still in position and completely ankylosed with the vertebræ (see *sr*, fig. 17). These ribs are short, compressed plates with expanded articular ends. Inferiorly the first rib articulates with the centra of the last dorsal and first sacral, more especially the latter. Above, the rib has become coossified with the buttress and diapophysis of sacral one. This broad, vertical plate is directed outward and somewhat backward. Its outer end is expanded antero-posteri-

[a] Amer. Journ. Sci., XLVIII, 1894. pp. 88, 89.

orly and coalesces with the similarly expanded end of the second rib, thus inclosing a subcircular sacral foramen (*f* and *f*[1], fig. 17). If present, the other ribs would probably repeat this arrangement, and there would be a row of at least four of these foramani—possibly five, if the transverse of the first sacro-caudal reaches the intero-posterior border of the ilium, which I doubt. The outer coalesced ends of ribs one and two exhibit a wide articular area, looking downward and outward, for articulation with the ilium. Two of these ribs were found with specimen No. 2210, but both were detached, although not far removed from their positions in the sacrum. It would appear from the evidence of these two individuals that in the young they remain distinct, but in the adult become completely fused with the sacrum.

After a study of these processes as represented in *Camptosaurus*, it is at once apparent that they are derived from centers of ossification entirely distinct from those which give origin to the centra or their neurapophyses. Inasmuch as the diapophyses are distinct from the sacral ribs, as shown in some individuals, there appears no good reason why, in this group at least, they should not be considered true ribs, modified to fit the exigencies of their position. The sacro-dorsal in *Camptosaurus*, as in *Triceratops*, is considered to be without parapophyses. The parapophyses of the second sacral, however, might be considered the articular area on the pedicle of the arch below the diapophyses, extending down on to the centrum which supports the lower articular portion of the sacral rib. The additional support given this rib by the posterior area of the first sacral centrum I should consider as being homologous with the demi-facets found in the dorsals of certain groups of the mammalia. The fact that a single-headed rib is borne by the last dorsal shows without question that the first sacral rib would, as shown previously, pertain to sacral one.

While Hatcher [a] has shown the probability of the supports for the ilia in the Sauropoda being the coalesced dia- and parapophyses, his arguments do not appear conclusive, and in view of the evidence here presented I am convinced that in *Camptosaurus* at least the existence of true sacral ribs is fully determined.

When the centra are articulated the ventral surface as a whole is slightly arched, its outline being rendered sinuous by the constriction of the middle of the centra and the prominence of their terminal borders. In *Camptosaurus*, as shown by the sacra considered in the previous pages, the sacrum is composed of either four or five vertebræ, which will receive further attention in the present paper when the several species are discussed.

[a] Mem. Carnegie Mus., II, No. 1, Nov., 1903, pp. 21, 22.

The caudal vertebræ.—Thirty-three caudal vertebræ were found associated with Cat. No. 4282, U.S.N.M. Their position in the quarry in relation to one another is clearly shown in Plate 6. With the type of *C. nanus* (Cat. No. 2210, U.S.N.M.) were 34 caudals, most of them still connected by the adhering matrix. After careful consideration of the evidence presented by the above series, it is estimated that in *Camptosaurus* there would be at least 44 caudal vertebræ in the complete tail.

As found, there were interruptions (see Plate 6) in the anterior series of No. 4282, but upon assembling the scattered parts it is believed they represent an unbroken string as far back as the sixteenth caudal. Between the sixteenth (quarry number 208) and the distal series (beginning with quarry number 235, see quarry map, Plate 6), it is estimated there are five vertebræ missing.

The above estimate is based not only upon the proportionate ratio of decrease in size necessary to fill the gap, but also upon the caudal series of *C. nanus*, which has this region intact and still connected by matrix. The terminal caudals are unknown, but the last one of the series (estimated to be the thirty-eighth, quarry number 234) has a transverse diameter on the posterior end of 13 mm. It is not likely there was a series of rod-like caudals, as found in some members of the Opisthocoelia,[a] but rather that the tail ended more abruptly like that of *Stegosaurus*, that is, with a pointed terminal caudal, as shown by three specimens in the National Museum.

In No. 4282, U.S.N.M., the first caudal (*sc*, fig. 17), or, as it might be better termed, sacro-caudal, is united to the sacrum by suture, being more securely joined by the peg-and-notch articulation (see fig. 17). It is considerably shortened antero-posteriorly, and, viewed from the end, is cylindroid in outline. A heavy subcircular rib, or transverse (*tr*, fig. 17), is attached by suture to the neural process just above the neuro-central suture. The neural canal is contracted to a small, circular passage having a diameter of 15 mm. On the median ventral surface are two subcircular depressions separated by a median longitudinal ridge or keel. The neural arch is much compressed transversely. The anterior zygapophyses are placed quite close together, their articular faces being nearly vertical, while the posterior are placed more obliquely and slightly overhang the end of the centrum. The spinous process of this vertebra is missing. The second caudal bears the first chevron (see *cf.*, fig. 18). Its centrum has a cupped anterior surface, the whole contour of this end being concave dorso-ventrally. The posterior articulating surface is more rounded, with an oblique ventral surface for the attachment of the chevron. This end is only slightly concave on the

[a] J. W. Holland, Mem. Carnegie Mus., II, 1906, p. 253.

upper median face. The lateral surfaces of the centrum are evenly concave antero-posteriorly. The small, circular neural canal extends down somewhat obliquely from front to back, a peculiarity present in a few of the succeeding vertebræ, and appears to indicate a rapid dropping of the tail as it leaves the sacrum. The neural arch is low and firmly attached to the centrum by broadly expanded pedicles. The transverse processes spring from the sides of the neural arch just above the neuro-central suture (see *s′*, fig. 18), extending out at right angles to the centrum on a level with the neural canal, not so high above it as shown in Marsh's restoration of *C. dispar* (see Plate 18).

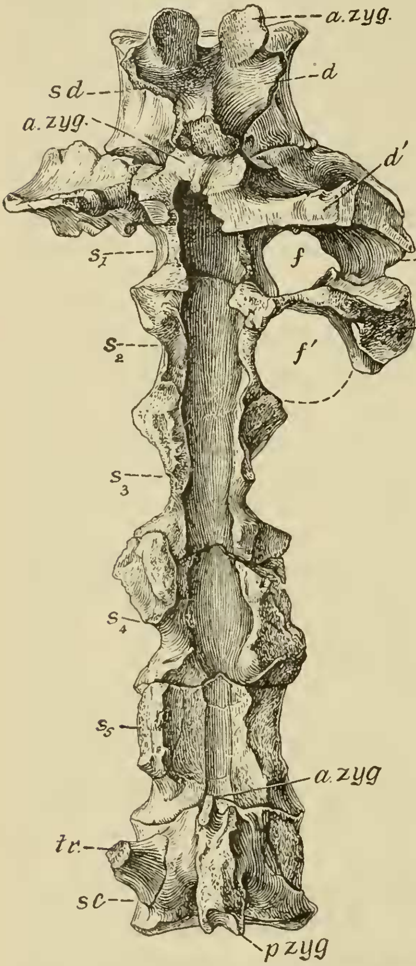


FIG. 17.—SACRUM OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE; SEEN FROM ABOVE. *a. zyg*, PREZYGAPOPHYSES; *d*, DIAPOPHYSIS OF 16TH OR SACRO-DORSAL; *d′*, DIAPOPHYSIS OF SACRAL ONE; *f*, *f′*, FORAMINA BETWEEN THE SACRAL RIBS; *p. zyg.* POSTZYGAPOPHYSES; S_1, S_2, S_3, S_4, S_5, SACRAL VERTEBRÆ ONE TO FIVE, RESPECTIVELY; *Sc*, SACRO-CAUDAL; *Sd*, SACRO-DORSAL; *Sr*. SACRAL RIBS; *tr*, TRANVERSE PROCESS OF SACRO-CAUDAL.

It has also been determined from these specimens that Marsh's representation of this region on Plate 56, "Dinosaurs of North America," is in error in the following respects: The neural arches are too high: the spinous processes are too straight and do not decrease in height rapidly enough after leaving the sacrum; their bases should show the antero-expansion of the base of the spine, and their tops should be directed at more of an angle posteriorly. The spinous process of the second caudal rises as a high, thin, backwardly directed blade of bone (see *s*, fig. 18), terminated by a slightly thickened end, which is gently rounded antero-posteriorly. There is a prominent widening of the base of the spine by the development on the anterior margin of a thin septum of bone which subsides rapidly above. This anterior development of the base of the spine becomes less and less pronounced, only a vestige remaining on the thirteenth caudal.

From the third to the tenth the centra gradually increase in length, the articular ends also undergo modifications from the vertically elongated type anteriorly to the compressed medially, and to the cylindroid of the posterior half, both ends of nearly all of the centra being slightly concave.

Flattened transverse processes are present on the first twelve vertebræ counting from the sacrum. The third is believed to bear the longest transverse, behind which they gradually shorten until, on the thirteenth, there remains only an inconspicuous tubercle. The sup-

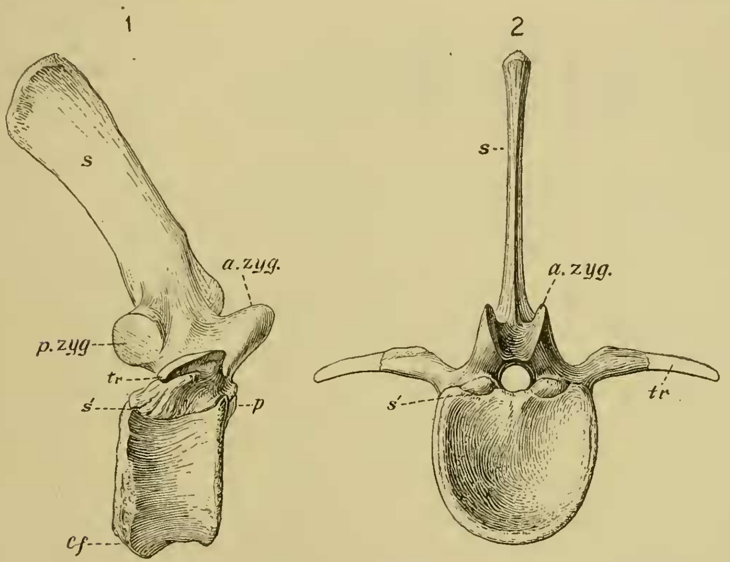


FIG. 18.—(1) SECOND CAUDAL VERTEBRA OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE; SIDE VIEW. (2) ANTERIOR VIEW OF SAME; *a. zyg*, PREZYGAPOPHYSES; *cf*, FACET FOR FIRST CHEVRON; *p*, RUDIMENTARY PEG-LIKE PROJECTION; *p. zyg*, POSTZYGAPOPHYSIS; *s*, NEURAL SPINE; *s'*, NEURO-CENTRAL SUTURE; *tr*, TRANSVERSE PROCESS.

pression of the transverse process is soon followed by the disappearance of the neuro-central suture, which becomes very indistinct. The point of attachment of the transverse processes gradually moves backward from the anterior lateral surface in the proximal caudals to a postero-lateral position in those more distal. As Hatcher [a] has pointed out in *Haplocanthosaurus*, so in *Camptosaurus* the transverse processes are derived from centers of ossification distinct from those which gave origin to either the centra or their spinous processes. This fact may be considered by some as proof that these are not transverse processes but perhaps might be considered caudal ribs

[a] Mem. Carnegie Mus., II, 1903, p. 22.

homologous with those of the sacral region. The compressed, blade-like spines of the anterior caudals decrease rapidly in both height and width antero-posteriorly to a compressed, rod-like spine on the eighth.

The spines gradually reduce in size posteriorly, at the same time becoming more and more depressed until in the smallest and most posterior they are nearly parallel with the longer axes of the centra (see fig. 19). As found in No. 4282, they persist almost to the end of the tail as small bony rods with compressed ends, without expansion, which extend well back over the succeeding vertebra.

The anterior zygapophyses gradually lengthen posteriorly until, in the distal caudals, as shown in fig. 19, they consist of two slender finger-like processes which extend forward and lap along the base of the neural spine of the preceding vertebra. The posterior zygapophyses of the anterior caudals slightly overhang the ends of the centra but gradually come to occupy a higher position on the spine, and with the increased slant of the latter, they overhang considerably. The zygapophyses also grow smaller until just back of the middle caudal region there is no well defined articular area, the zygapophyses simply clasping the base of the spine, as mentioned above.

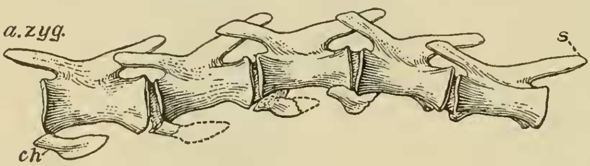


FIG. 19.—POSTERIOR CAUDAL VERTEBRÆ WITH CHEVRONS (30TH TO 34TH, INCLUSIVE), CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE; SIDE VIEW; *a. zyg.* PREZYGAPOPHYSIS; *ch*, CHEVRON; *s*, NEURAL SPINE.

The anterior vertebræ have oblique facets on both ends of the centra, but in the distal region there remain only weak facets on the ventral posterior ends. The anterior chevron facets are the first to disappear.

Principal measurements of vertebræ.

Vertebræ.	Greatest length of centra.			Greatest transverse diameter, posterior ends.			Remarks.
	U.S.N.M. No. 4282.	Yale Museum No. 1877.[a]	U.S.N.M. No. 2210.[b]	U.S.N.M. No. 4282.	Yale Museum No. 1877.[c]	U.S.N.M. No. 2210.	
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	
Atlas	....	24	....	....	56	....	
Axis	....	53	20	....	53	18	Anterior end No. 2210 =22 mm., transverse diameter.
3	70	61	23	[d]40	46	19	
4	70	53	24	....	45	[d]21	
5	....	59	26	....	47	22	
6	....	50	26	....	56	22	
7	67	52	26	70	54	23	Greatest height (with spine) of No. 4282, taken at center, 93 mm.
8	77	62	25	66	58	24	Greatest height (with spine) of No. 4282, taken at center, 91 mm.

[a] No. 1877=holotype *C. dispar*.
[b] No. 2210=holotype *C. nanus*.
[c] No. 1877*a*=paratype *C. dispar*.
[d] Estimated measurements from mutilated specimens.

Principal measurements of vertebræ—Continued.

Vertebræ.	Greatest length of centra.			Greatest transverse diameter, posterior ends.			Remarks.
	U. S. N. M. No. 4282.	Yale Museum No. 1877.	U. S. N. M. No. 2210.	U. S. N. M. No. 4282.	Yale Museum No. 1877.	U. S. N. M. No. 2210.	
	mm.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	
9	70	61	26	68	64	[a] 23	Greatest height (with spine) of No. 4282, taken at center, 95 mm.
Dorsal 1	63	61	24	60	[a] 61	22	
2	70	.....	25	62	.....	20	
3	75	.....	26	66	.....	21	Greatest height (with spine) of No. 4282, taken at center, 183 mm.
4	72	.....	25	60	.....	22	
5	74	.....	28	62	.....	22	
6	75	.....	30	66	.....	23	
7	75	.....	29	70	.....	24	
8	75	.....	29	69	.....	.....	
9	70	.....	31	70	.....	27	
10	70	.....	30	70	.....	[a] 28	
11	77	.....	30	78	.....	[a] 32	
12	80	.....	31	80	.....	33	
13	75	.....	31	90	.....	[a] 35	Greatest height (with spine) of No. 4282, taken at center, 260 mm.
14	65	Yale Museum.	27	94	.....	36	
15	57	No. 1877a	30	107	.....	47	
16	66	86	32	118	125	48	Greatest height (with spine) of No. 1877a, taken at center, 330 mm.
Sacral 1	73	85	30	118	119	.....	Greatest height (with spine) of No. 1877a, taken at center, 328 mm.
2	75	82	31	[a] 77	100	34	
3	75	76	30	90	90	[a] 33	
4	70	80	30	[a] 95	110	.....	
5	70	.....	.....	101	.....	.....	
Caudals:							
1	62	.....	28	101	.....	[a] 37	
2	60	.....	25	[a] 85	.....	36	Greatest height (with spine) of No. 4282, taken at center, 270 mm.
3	57	.....	26	83	.....	34	
4	59	.....	27	77	.....	32	
5	60	.....	25	76	.....	29	
6	60	.....	26	[a] 70	.....	28	
7	60	.....	25	82	.....	26	
8	61	.....	26	67	.....	26	
9	71	.....	25	66	.....	25	
10	70	.....	25	51	.....	25	
11	69	.....	[a] 24	54	.....	24	
12	66	.....	26	54	.....	23	
13	64	.....	26	54	.....	24	
14	69	.....	27	60	.....	24	
15	71	.....	26	58	.....	24	
16	73	.....	26	[a] 58	.....	.....	
17	.....	.....	26	.....	.....	22	
18	.....	.....	26	.....	.....	22	
19	.....	.....	25	.....	.....	22	
20	.....	.....	24	.....	.....	24	
21	.....	.....	24	.....	.....	[a] 23	
22	62	.....	23	[a] 48	.....	22	
23	60	.....	21	48	.....	22	Greatest height (with spine) of No. 4282, taken at center, 68 mm.
24	60	.....	21	.....	.....	[a] 21	
25	56	.....	21	.....	.....	20	
26	55	.....	.....	40	.....	.....	
27	55	.....	.....	.....	.....	.....	
28	54	.....	.....	37	.....	.....	
29	52	.....	.....	.....	.....	.....	

[a] Estimated measurements from mutilated specimens.

Principal measurements of vertebræ—Continued.

Vertebræ.	Greatest length of centra.			Greatest transverse diameter, posterior ends.			Remarks.
	U. S. N. M. No. 4282.	Yale Museum No. 1877.	U. S. N. M. No. 2210.	U. S. N. M. No. 4282.	Yale Museum No. 1877.	U. S. N. M. No. 2210.	
Caudals—Continued.	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*	
30	50						
31	49						
32	47						
33	47			22			
34	43			22			
35	41			20			
36	39			17			Greatest height (with spine) of No. 4282, taken at center, 32 mm.
37	39			15			
38	38			13			

THE CHEVRONS.

Chevrons from the anterior, middle, and posterior parts of the tail were found in position with the caudals of Cat. No. 4282, U.S.N.M.

The anterior chevrons are longer than the spinous processes and are reduced more slowly posteriorly. They are Y-shaped, with expanded articular ends, the surfaces of the opposite sides being bridged across. Viewed laterally (see 1, fig. 20), this end is wedge-shaped, the posterior facet being the larger. The chevrons articulate intervertebrally with beveled articular surfaces on the ends of the centra. The opening between the branches, as compared with the chevrons of other members of the Dinosauria, is much constricted both transversely and longitudinally. The free end is expanded and flattened. The shaft is straight, not curved backward, as in many reptiles, in this respect similar to the anterior chevrons found in the trachodonts. With the exception of being smaller and having the articular end about evenly divided between the anterior and posterior facets, and the lower part of the shaft curved backward, the median chevrons are very similar to those described above.

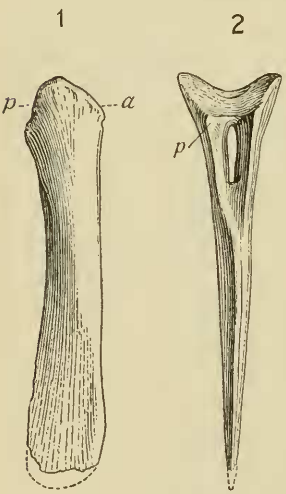


Fig. 20.—(1) Anterior chevron of Camptosaurus dispar Marsh. Cat. No. 5818, U.S.N.M.; ¼ nat. size; side view; (2) posterior view of same: *a*, anterior; *p*, posterior.

Those of the more posterior region, however, are considerably altered from the above types, as will be seen by reference to fig 19.

The articular ends of the opposite sides are separate and when in position unite more especially with the anterior than with the posterior vertebra. The opening between the branches is proportionately more elongated, and the free end is thin and expanded into a broad, knife-like end. The chevron found articulated between quarry numbers 220 and 221 of the distal series is 52 mm. in length. This would be the twenty-fourth of the series counting from the sacrum. The twenty-eighth is 45 mm. (see *ch*, fig. 19) in length, and the thirty-first is only 25 mm. The free end is rounded from the lower margin of the opening up to the dorsal border, as a thin, sharp keel, well shown in *ch*, fig. 19. In a rudimentary form they appear to have persisted as far back as the thirty-sixth caudal, as indicated by imperfectly developed chevron facets on the centra.

THE RIBS.

In *Camptosaurus* there are present cervical, dorsal, sacral, and caudal (?) ribs. Excepting the atlas, all of the cervical vertebræ, as shown by the distinct tubercular and capitular facets, bear double-headed ribs.

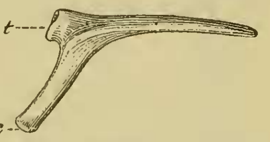


FIG. 21.—EIGHTH CERVICAL RIB OF LEFT SIDE CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE; SIDE VIEW; *c*, CAPITULUM; *t*, TUBERCULUM.

Cervical ribs.—The capitulum is in all cases carried on the longer of the two anterior branches. This branch, which is comparatively short on the anterior cervical ribs, gradually lengthens posteriorly, being considerably produced on the eighth and ninth of the series (see *c*, fig. 21). The posterior branch terminates as a somewhat rounded, pointed end. As shown by the single facets on the posterior ventral surface of the intercentrum of the atlas (see *r*, fig. 12), it appears to have carried a single-headed rib, as in the crocodile.

Anterior cervical ribs pertaining to Cat. No. 5473, U.S.N.M., show the point where the two anterior branches unite as a broad rounded base with very short, pointed posterior branch (see Plate 12). In Cat. No. 4282, U.S.N.M., the ribs of the eighth and ninth cervicals were found articulated and in a fairly good state of preservation. These are thin, flattened bones, without pronounced anterior indentation. The capitular process is moderately long, with convex articular end, while the tubercular process is short, heavy, and has a concave articular end. When articulated their posterior extremities are directed backward, outward, and downward, somewhat below the horizontal.

Dorsal ribs.—With the exception of the last dorsal, or, better, sacro-dorsal, all of the other dorsal vertebræ bear double-headed ribs. The ribs of the anterior portion of the thoracic cavity are considerably curved, especially near their upper extremities. The capitulum is borne on a heavy, rounded process, being well separated from the weaker step-like tuberculum developed on the supero-posterior border. Posteriorly, however, the capitular facets on the vertebræ gradually shift their position nearer to the tubercular facet, and thus the distance between the capitulum and tuberculum of the rib is gradually lessened. Fragmentary ribs found articulated with the dorsals of Cat. No. 4282, U.S.N.M., shows that the seventh (counting from the last cervical) bears the heaviest rib of the series. The posterior ribs are more slender, straighter, and shorter than those anterior.

The sacro-dorsal mentioned above must have borne a short, single-headed rib, as indicated by the single capitular facet on the other extremity of the weak transverse process (see fig. 39 and *a*, Plate 13), but there is no indication of ankylosis of the rib with the end of the transverse, as Hulke[a] has found in this region of *Hypsilophodon foxii*.

The sacral ribs will be found described in connection with the sacrum on page 237, and the caudal ribs, or transverse processes, with the caudal vertebræ.

OSSIFIED TENDONS.

In the matrix surrounding some of the vertebræ of No. 4282 there are preserved a number of flattened, rod-like ossified tendons. In this individual they were found as far forward as the eleventh dorsal, and in the type of *C. nanus*, on the eighth. These ossifications are also present in the sacral region, and they undoubtedly occurred along the spinous processes of the anterior caudals, although from the condition of the available material this point can not be determined. The ends are much flattened and divided into a number of ray-like points. They do not appear to have had any such development as found in either *Trachodon* (*Claosaurus*) or *Triceratops*. These ossifications are shown at *ot* in fig. 39.

In a paper on *Hypsilophodon*,[b] Baron Nopcsa calls attention to the presence of ossified tendons along the backbone of that animal, and he also shows that these ossifications are present in all of the British predentate reptiles, with the exception of *Scelidosaurus*. In the American members of this group they were first observed by Marsh[c] in *Trachodon* (*Claosaurus*), and later in members of the Ceratopsia by Hatcher.[d]

The arrangement of the tendons along the posterior dorsal vertebræ and over the sacrum is well represented in Plate 19, where they are shown as found in the matrix. Their arrangement approximates the conditions present in *Iguanodon bernissartensis* as figured by Dollo.[e]

[a] Phil. Trans. Roy. Soc. London, CLXXIII, 1882, p. 1047.

[b] Geological Magazine, May, 1905, pp. 203–208.

[c] Amer. Journ. Sci., XLIV, Oct. 1892, p. 345.

[d] Mon. U. S. Geol. Surv., XLIX, 1907, p. 51, fig. 48.

[e] Bull. Bruxelles Mus. Roy. d'Hist. Nat. de Belgique, II, 1883, pl. v.

THE SHOULDER GIRDLE.

The scapula and coracoid are the only elements preserved in the pectoral arch. Nothing representing either a clavicle or a sternal has yet been found, although it appears quite probable, as will be shown later, that such may have been present, notwithstanding Marsh's statement that the sternum in *Camptosaurus* was unossified.

The scapula.—The scapula is a moderately long bone, and when not flattened by crushing has a decided bow in the shaft which conforms closely with the outward curve of the body cavity (see fig. 22), and which throws the articulated coracoid well in under the chest. Just above the heavy, expanded articular end the shaft contracts rapidly, but again gradually expands antero-posteriorly toward the upper end. The backward extension of the blade being the greater, the median external portion of the shaft is gently rounded transversely, while the thin expanded upper extremity of the blade is quite flat. The upper end terminates as a slightly thickened rounded border. The anterior border is sinuous and has a sharp edge, while the posterior is rounded except in its upper third, which is comparatively thin and sharp. The internal surface is smooth and flattened, with a decided bow from end to end, as mentioned above. The articular end being expanded both vertically and transversely, is heavy and massive. A prominent ridge is developed on the lower outer surface, which contributes to the formation of the posterior lip of the glenoid fossa (see *g*, fig. 23). On the anterior margin, above the articulation for the coracoid, is a strong protuberance with a well-defined triangular facet, adapted to the support of a clavicle, if such a bone were present. This feature is clearly shown in the right scapula of No. 5473, U.S.N.M., and is also seen in other scapulæ in the same collection. A somewhat similar protuberance is noticed on the scapulæ of the larger trachodonts. A short but prominent ridge rises on the external face of the projection just described, but gradually subsides upon reaching the flattened surface of the shaft. The articular end presents a thickened, roughened, deeply pitted sutural articulation for the coracoid, with which it has never yet been found firmly coossified. Inferiorly and posterior to this border is a smooth, concave articular surface which, with a similar surface on the coracoid, forms the glenoid fossa.

FIG. 22.—POSTERIOR VIEW OF ARTICULATED SCAPULA AND CORACOID OF CAMPTOSAURUS DISPAR MARSH. CAT. NO. 5473, U.S.N.M.; ⅛ NAT. SIZE; *c*, CORACOID; *gl*, GLENOID CAVITY; *s*, SCAPULA. FROM A PHOTOGRAPH.

On the median internal surface near the border of the articular end for the coracoid is a narrow, longitudinal groove which passes outward diagonally to meet the foraminal notch in the coracoid.

FIG. 23.—LEFT SCAPULA OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE; VIEWED EXTERNALLY; *c*, SURFACE FOR CORACOID; *g*, GLENOID CAVITY. FROM A PHOTOGRAPH.

This groove is present on all of the scapulæ studied, and, so far as I am aware, is only found in the Dinosauria among the members of the Camptosauridæ and the Laosauridæ.

Measurements of Specimen Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left scapula and coracoid	595
Greatest length of scapula	482
Greatest breadth of scapula	175
Least breadth of scapula	63
Greatest expanse of glenoid cavity	83

The coracoid.—The coracoid is a small subrectangular bone, with the anterior and inferior borders turned inward, forming a moderately deep concave internal surface both antero-posteriorly and vertically. Externally the surface is convex in both directions. There is a broad notch on the inferior border. Anterior to this notch the border is thickened on the antero-infero angle, the surface being roughened, more especially the internal, and is thus indicative of the presence of cartilaginous attachment of sternal elements. The border posterior to the notch is especially thickened and represents the coracoid component of the glenoid fossa (see *c*, fig. 24). The inferior smooth articular part of the posterior border is separated from the rugose surface for union with the scapula by a deep, foraminal notch, which on some individuals is nearly closed. This notch passes through diagonally, emerging on the postero-internal border, as in *Iguanodon*. In none of the specimens examined did it exist as a well-defined

FIG. 24.—LEFT CORACOID OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ¼ NAT. SIZE. EXTERNAL VIEW. *a*, ANTERIOR BORDER; *b*, BORDER FOR ARTICULATION WITH SCAPULA; *c*, BORDER OF GLENOID CAVITY. FROM A PHOTOGRAPH.

foramen, as found in other members of the Dinosauria and as indicated by Marsh in his illustrations of this element. The superior border presents a thin, sharp edge, while the anterior is more rounded and roughened, with a thickened portion at the antero-supero angle.

Measurements of Specimen Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left coracoid	115
Greatest width of left coracoid	156

THE FORE LIMB.

The humerus.—The humerus is comparatively short, being somewhat expanded at both extremities, more especially the proximal.

Fig. 25.—Left humerus of Camptosaurus browni. Holotype. Cat. No. 4282, U.S.N.M.; ¼ nat. size. Front view. *d*, deltoid crest. From a photograph.

Fig. 26.—Left humerus of Camptosaurus browni. Holotype. Cat. No. 4282, U.S.N.M.; ¼ nat. size. Back view. *h*, head. From a photograph.

The head is situated in about the middle of the proximal end and is produced considerably backward beyond the posterior border of the shaft (see *h*, fig. 26). It has a smooth, subspherical, articular surface from which a ridge-like swelling passes down into the posterior surface of the shaft. There is a heavy radial crest developed on the antero-external border just above the middle of the shaft which renders the anterior aspect of the surface concave. The crest (see *d*, fig. 25) appears to occupy a lower position on the shaft than it does on the humerus of *Iguanodon*. The shaft is somewhat twisted and planes passed through the longer axes of the articular ends would cut one another at a slight angle. The outer surface of the radial crest is roughened for muscular insertion. Below the crest the shaft is constricted and is subcircular in cross section. The internal border is regularly curved from end to end, while the external is angularly convex. The radial and ulnar condyles are well defined and posteriorly are separated by a broad, shallow depression which passes somewhat up the shaft of the bone. There is also a shallower depression between them on the distal anterior surface of the bone. The articular ends of the humerus are quite rugose in the individual here described.

Measurements of Specimen, Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left humerus	360
Greatest width proximal end	116
Greatest width dorsal end	82

The ulna.—The ulna is heavy above and but little expanded on the distal end. Its length slightly exceeds that of the radius, but is shorter than the humerus, differing in the latter particular from *Trachodon*, in which the ulna exceeds the humerus in length. There is the beginning of a massive olacrenon (see fig. 41), but it extends but little above the articular surface for the humerus. Viewed proximally the end is subtriangular in outline. The middle of the shaft in cross section is elliptical. The distal end is somewhat expanded (see *ul*, fig. 27), the greatest diameter being transverse. The lower internal surface is slightly roughened and flattened for contact with the grooved external surface of the distal

Fig. 27.—Right radius, ulna, and manus of Camptosaurus browni. Holotype. Cat. No. 4282, U.S.N.M.; about ¼ nat. size. Front view. Shows position of elements as found in the quarry. *i*, intermedium; *ra*, radius; *u*, ulnare; *ul*, ulna. From a photograph.

part of the radius (see fig. 41). The articular ends of this bone are smoother than the corresponding parts of the humerus.

Measurements of Specimen, Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left ulna	262
Greatest width proximal end of ulna	75
Greatest width distal end of ulna	62

Radius.—The radius is more slender and somewhat shorter than the ulna. It is slightly expanded at the extremities, more especially the proximal end (see *ra*, fig. 27). In cross section the shaft is subcircular and continues so for most of its length. On the distal external surface of the bone is a longitudinal groove which receives the roughened border of the distal end of the ulna when articulated. Viewed from the distal end the extremity is heavy and roughly subcrescentic in outline, with an oblique end, the surface of which looks downward and outward and fits closely to the reverse bevel of the radiale. This is clearly shown in fig. 27, which represents the forearm and carpus of the right fore limb of *C. browni*, Cat. No. 4282, U.S.N.M.

Measurements of Specimen, Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left radius	232
Greatest width of proximal end	58
Greatest width of distal end	41

THE FORE FOOT.

In *Camptosaurus* there are five digits in the manus, supported by eight carpalia. The carpus has a simple arrangement, that is, a proximal row of three bones—the radiale, intermedium, and ulnare—and a distal row of five. The number of phalanges, beginning with the first digit or pollex, as correctly determined by Marsh, is 2, 3, 3, 3, 2.

The detailed description to follow is based upon a fore foot of *Camptosaurus dispar*, Cat. No. 4277, U.S.N.M., from quarry 13, near Como, Albany County, Wyoming. The foot is complete with the exception of phalanges one and two of Digit I, and two and three of Digit IV. The missing parts, with the exception of the ungual of Digit I, which is unknown, will be described from other feet in the National Museum. This foot was found articulated in the field and was so received in the laboratory, and on that account there can be no question regarding the relative position of its elements. The form and proportions of the various bones of the manus are well shown in fig. 28.

The carpus.—In the carpus of the typical specimen of *Camptosaurus dispar*, No. 1877, Yale Museum, Marsh recognized nine carpal bones, but I am unable to detect more than eight. Specimens in the

National Museum also show but eight. It appears that the number will vary in fully adult individuals, due to the fusion of the smaller with the larger members.

The proximal row forms two distinct concave surfaces for articulation with the distal ends of the radius and ulna. These articulating surfaces are clearly defined, as in many of the fore limbs of the mammalia, an unusual condition as is well known to all who have attempted to articulate the limb and foot elements of most members of the Dinosauria. The contour of these opposing articular ends is distinctly shown in fig. 27, which represents the right fore foot of *C. browni*, and is reproduced from a photograph of the specimen as it was found in the quarry.

The *radiale* (*r*) is an irregularly shaped, block-like bone, the most robust element of the carpus. Its proximal end forms the chief support for the radius, the distal end articulates with Metacarpal I and carpalia one, two, and three, and externally with the internal border of the intermedium, with which it is often coossified (see fig. 27). The union with Metacarpal I is at an angle of nearly 45° to the main axis of the foot, and in all of the feet studied, where these elements were preserved, they were found to be firmly ankylosed, particularly along the anterior surfaces, as will be seen in fig. 28. This digit was thereby rendered immovable, which is suggestive of the "spike-like" digit of the allied *Iguanodon*.

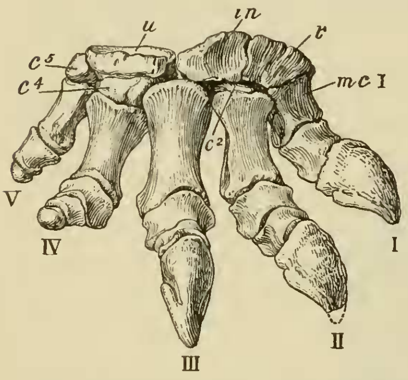


Fig. 28.—Right fore foot, Camptosaurus dispar Marsh. Cat. No. 4277, U.S.N.M.; ¼ nat. size. Seen from the front. c^2, carpal two; c^4, carpal four; c^5, carpal five; *in*, intermedium; *mc I*, metacarpal I; *r*, radiale; *u*, ulnare; I to V, digits one to five. Ungual of first digit restored.

The *intermedium* (*in*) viewed from the front is subtriangular in outline, the apex pointing toward the ulnare (see *in*, fig. 28.) Its dorsal surface articulates with both the radius and ulna, but more especially with the latter; ventrally it is supported by Metacarpal III, and a small, irregularly shaped element on the posterior internal part of this end which probably represents C_3. Although apparently in position in this foot, in the right fore foot of another specimen (Cat. No. 5473, U.S.N.M.), C_3 lies more over the proximal end of Metacarpal III, which somewhat confirms its identification. This element, however, is about equally divided between the intermedium and radiale.

The *ulnare* (*u*) is a cushion-like bone, its transverse being greater than the antero-posterior diameter (see *u*, figs. 27 and 28). It has a smooth, concave proximal end forming the chief support of the ulna. The anterior surface is convex transversely, while the posterior is concave. It articulates with the intermedium by two facets on either extremity of the internal border. The intervening border being concave is not in contact with that of the intermedium.

There are five small elements in the distal row of the carpus. Carpale one is a small ossicle-like bone wedged in between the ends of Metacarpal 1 and the radiale on the posterior side. It is not visible from the front aspect. In the forefoot of specimen No. 5473, this element was in position but remained as a distinct bone. In No. 4277, however, it is fused with both the radiale and Metacarpal I and is hardly recognizable.

The second carpale in No. 4277 is a small, flattened, rectangular element which was retained in position on the proximal end of Metacarpal II. Its thin, anterior border is visible in fig. 29 between the radiale and Metacarpale II.

The third carpale is a wedge-shaped element coossified about equally with the posterior part of the surfaces of the radiale and intermedium. It articulates slightly with Metacarpal III, and although in other specimens it is visible from a front view of the foot, in this one it is not.

Carpale five, seen from the front, is a lozenge-shaped element interposed between the outer distal surface of the ulnare and the proximal end of Metacarpal V. Marsh has represented this element in the foot of *C. dispar* as contributing to the ulnar surface, but in the specimen here described, an outer extension excludes it from the ulnar surface.

The metacarpus.—Metacarpal I is much the shortest element of the series and in adult individuals is always fused with the radiale. The inner border of the proximal end rises to the level of the dorsal surface of the radiale and contributes slightly to the articulating surface for the radius. The distal end is convex dorso-ventrally with a pronounced median depression or groove. The short shaft is angular in cross section, being wider than deep. Fore and aft on the external lateral margin of the proximal end are two antero-posteriorly elongated facets which articulate with corresponding facets on the internal margin of Metacarpal II.

Metacarpal II is more than twice the length of the preceding and more slender. The proximal end is subtriangular in outline, its antero-posterior diameter being the greater. The articular surface of this end is comparatively smooth and gently convex antero-posteriorly. The shaft is somewhat constricted but expands again at the distal end, more especially in its transverse diameter. The external border of the distal end is produced distally below the internal, which deflects the phalanges of this digit mesially. The posterior border is deeply concave transversely, being a continuation posteriorly of the median depression of this end. The proximal half of the external lateral surface is concave antero-posteriorly, forming a depression which receives a rugose convex surface on the internal lateral surface of Metacarpal III. The distal lateral surfaces are quite smooth.

Metacarpal III is the longest and most robust element of the five. Its proximal end is subtriangular in outline, being longer than wide. The shaft is constricted and at its smallest part would be subcircular in cross section. The distal end is expanded both antero-posteriorly and transversely. Like Metacarpal II this end is convex antero-posteriorly and concave transversely, although the median depression is not so pronounced as in Metacarpals I and II. The external lateral surface of the proximal end is roughened and during the life of the animal it probably had direct cartilaginous articulation with Metacarpal IV. As mentioned above, the proximal end articulates principally with the intermedium and slightly with carpale three.

Metacarpal IV is shorter and more slender than Metacarpal II, the shaft being more rounded. Viewed from above, the proximal end is subtriangular and has a smooth concave end which articulates closely with the distal end of carpale four. The distal end is proportionately less expanded than the preceding metarcarpals, and unlike them shows no pronounced median depression except on the anterior border.

Metacarpal V is the most slender of the series, although longer than Metacarpal I. Seen from above the proximal end is triangular and like Metacarpal IV has a smooth, transversely concave articular surface for union with carpale five. On the internal lateral surface near the proximal end is a shallow concave depression which articulates with an outward projection on the postero-external angle of the proximal end of Metacarpal IV, forming rather a weak union with that digit. The shaft is constricted, especially antero-posteriorly, which gives it a flattened aspect. The distal end is but little expanded, being convex antero-posteriorly, without median depression.

Measurements of metacarpals of Specimen, Cat. No. 4277, U.S.N.M.

Metacarpals.	I.	II.	III.	IV.	V.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
Length	26	61	76	60	40
Breadth of proximal end	33	31	35	40	38
Breadth of distal end	30	35	37	32	25

Phalanges.—The phalangial formula beginning with the first digit is 2, 3, 3, 3, 2.

The proximal phalanx of the first digit is short, with lateral and dorsal surfaces quite evenly rounded and palmar surface flattened.

The internal side is longer than the external. The proximal articular end is concave supero-inferiorly, with a blunt median keel for articulation with the groove on the distal articular surface of Metacarpal I. The distal end is regularly convex supero-inferiorly and concave transversely. This description is based on the phalanx of the left forefoot of *C. browni.* The ungual of Digit I is missing on all of the feet studied, but in the specimen shown in fig. 29 this element has been provisionally restored.

The proximal phalanges of Digits II and III are short, stout, block-like bones. The proximal articular ends are concave supero-inferiorly, with a median concave depression. The second phalanges of the above digits are much shortened, with concave proximal and convex distal ends. The palmar surfaces are flattened and produced posteriorly into thin sheets which lie under the distal ends of the proximal phalanges of their respective digits. This posterior extension is especially pronounced in the second phalanx of Digit IV.

Digits II and III are terminated by relatively large, pointed unguals, which were undoubtedly sheathed in horny claws, as indicated by a pair of lateral grooves on each ungual. The ungual of Digit II is considerably depressed; the proximal end is subtriangular in outline with concave supero-inferior surface. The median dorsal surface is produced posteriorly and overhangs somewhat this articular end. The proximal end of this ungual of Digit III is higher than wide and in outline is irregularly rounded. The articular end is more deeply concave than ungual two. The anterior end is deflected toward the foot of the opposite side and is sharply pointed. The proximal phalanx of the fourth digit is much depressed, especially at the distal end, and expanded transversely at the proximal end. The articular surface of this end is concave supero-inferiorly with only a faint indication of a keel on the superior part of the median surface. The palmar surface is flattened. The transverse extent of the distal end is much less than the proximal. It is convex supero-inferiorly with a suggestion of a concave median groove. The second phalanx of this digit is very short and supports a small, rounded, hemispherical, terminal phalanx which in life was probably embedded within the integument of the foot. The proximal end of the latter is indicated by a concave surface.

The proximal phalanx of Digit V is the most slender of the series. The upper articular end is about evenly concave in both transverse and vertical directions and tapers without noticeable constriction to the distal end, which is convex supero-inferiorly. The terminal phalanx of this digit is an irregular button-like ossicle.

From the above description and figures of the manus of *Camptosaurus* it will be seen that the weight of the body was borne principally on the three median digits, and that through disuse the fifth was becoming atrophied. While this has not yet resulted in the elimination of any of the digits, yet the fifth is fast approaching a functionless condition.

Measurements of phalanges of Specimen, Cat. No. 4277. U.S.N.M.

Digits.	I.	II.	III.	IV.	V.
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
Greatest length first row of phalanges	[a] 21	26	34	26	23
Greatest length second row of phalanges		24	26	[a] 16	6
Greatest length third row of phalanges		[b] 48	[b] 50	[a] 10	......

[a] Measurements of elements of left forefoot of No. 4282, is a slightly smaller individual.
[b] Estimated, elements incomplete.

THE PELVIS.

The pelvis of *Camptosaurus*, as shown in Plates 15 and 16, is quite characteristic of the genus. It is composed of the three elements, the ilium, ischium, and pubis, usually found in the pelvis of the

Fig. 29.—Left ilium of Camptosaurus dispar Marsh. Cat. No. 5473, U.S.N.M.; ⅛ nat. size. External view. End of pubic peduncle missing. From a photograph.

Dinosauria. The long, slender post-pubis, reaching to the end of the equally long shaft of the ischium, is distinctive of this group. With the exception of the pubis, the parts described below are of specimen Cat. No. 4282, U.S.N.M.

The ilium.—The ilium is an elongated plate-like bone, resembling in most of its characteristics the corresponding element of *Iguanodon*. The preacetabular process is long, narrow, and compressed laterally. The ilia of this specimen lack the anterior termination, but in *C. dispar*, as shown by the ilium of Cat. No. 5473, U.S.N.M., the end is somewhat spatulate (see fig. 29). This long, slender process extends forward and outward, overhanging the posterior ribs. The superior border of the ilium is thickened and rounded transversely, and at the posterior end descends for a distance of 90 mm., at an oblique angle, gradually thickening to the point where it reaches the infero-internal plate. Viewed laterally the ilium has a width of 87 mm. from where the superior border begins to descend to the border where the inner shelf is given off. The acetabular arch is bounded anteriorly by a rather wide but slender pubic peduncle directed downward and forward. The posterior peduncle for the ischium is heavy, broadly swelled, with two roughened surfaces, more especially the posterior, which meet at an obtuse angle. The posterior and more inferior one, which is somewhat cupped, is for the articulation of the ischium. The roughened anterior surface appears to be for the attachment of the heavy pads of cartilage and ligaments which bound the pelvic bones together. Posterior to this process the inferior border is a sharp edge, which, as it extends backward gradually turns from a vertical to a nearly horizontal position, with a rounded, thickened, posterior termination. The upper half of the internal surface is smooth and gently concave from end to end. On the lower median internal surface are roughened cupped depressions, their greatest extent being vertical, for the articulation of the sacral ribs (see *x*, Plate 15). These surfaces are separated by narrow, smooth, concave, nonarticular tracts. A shallow, roughened longitudinal groove

FIG. 30.—LEFT ILIUM OF CAMPTOSAURUS BROWNI. HOLOTYPE. CAT. NO. 4282, U.S.N.M.; ⅙ NAT. SIZE. EXTERNAL VIEW. ANTERIOR END OF PREACETABULAR PROCESS RESTORED AFTER THAT OF THE LEFT ILIUM OF NO. 5473 (SEE FIG. 29). FROM A PHOTOGRAPH.

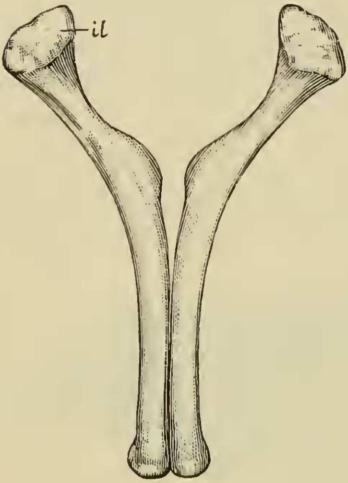
on the thickened internal edge of the shelf-like projection mentioned above, may be for the reception of the transverse process of the fifth sacral. The greatest vertical width of the ilium is over the ischiac peduncle.

The ilium is one of the most characteristic bones of the skeleton, and while the description given above shows all of the essential characters of the *Camptosaurus* ilium, it is found that in other species there are great differences of contour and proportion.

Measurements of Specimen, Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left ilium from posterior end to center of preacetabular notch	392
Greatest width over ischial process	75
Greatest width from middle of acetabulum	115
Greatest expanse of acetabulum	161

The ischium.—The ischium is larger than the pubis and distally consists of a slender rod-like shaft which curves downward with an expanded hammer-like end (see 1*a*, fig. 31). The distal ends appear to have been in contact as well as the borders of the lower half of their shafts. In *C. browni* this bone is lightly constructed, in this respect approaching the ischia of *C. medius.* The proximal end has a widely expanded Y-shaped extremity with two distinct articular faces (see *is*, Plate 16), the one for the posterior peduncle of the ilium being the heavier. Its articular surface is rugose and deeply cupped. The articular surface for contact with the pubis is borne on a thin, quadrilateral plate which extends downward and forward from the main shaft of the bone, and its upper antero-posterior concave border completes the acetabular boundary. The straight, truncated end of this plate is flat and thickened transversely, and when in position abuts against an opposing articular face on the posterior end of the pubis at about the middle line of the acetabulum. The lower anterior border is also thickened and is in contact with a depressed articular surface on top of the postpubis, just posterior to the pubic foramen. Behind, the expanded head contracts rapidly, but again widens on the inferior border into a thin, lip-like, downturned, obturator process, against which the rod-like shaft of the postpubis rests (see Plate 16). Below this process the shaft contracts and continues as a curved, rod-like shaft to the distal extremity. The position of the obturator process, well up toward the articular end, at once distinguishes the ischium of *Camptosaurus* from *Hyosilophodon foxii*, which has this process about midway between the two ends.



1*a*

FIG. 31.—ISCHIA OF CAMPTOSAURUS MEDIUS MARSH. SUPERIOR VIEW. YALE MUSEUM; ⅛ NAT. SIZE. *il*, ILIAC SURFACE; *1a*, DISTAL ENDS OF SAME. AFTER MARSH.

Measurements of Specimen, Cat. No. 4282, U.S.N.M.

	mm.
Greatest length of left ischium	545
Greatest width of proximal end	194
Greatest width of distal end	79

The pubis.—The description to follow is based on the pubis of *C. dispar*, No. 1878, Yale Museum, the postpubis from *C. medius*, No. 1880, Yale Museum (see *p′*, Plate 16).

As shown in fig. 32, the pubis in *Camptosaurus* is composed of a flattened prepubic element and an elongated, curved, slender postpubis. The anterior portion is a thin, flat, vertical blade of bone, when articulated extends forward, downward, and slightly outward. The superior border is gently concave antero-posteriorly, and near the proximal end expands transversely into a triangular, roughened surface for contact with the pubic peduncle of the ilium. The proximal end is expanded transversely, forming a heavy, concave end which bounds part of the anterior and inferior borders of the acetabulum.

The lower part of the proximal end has a rugose surface for contact with the antero-infero projection of the proximal end of the ischium. On the lower internal border of the proximal end the postpubic bar is developed, which extends backward and downward beneath and parallel with the ischium, reaching to the end of that bone. Between the anterior end of the postpubis and the posterior acetabular surface of the prepubis is a large pubic foramen, which, in some individuals at least, does not appear to have been entirely closed posteriorly. While the notch is closed in three individuals studied, the union of the two surfaces is not to coalescence, the suture in all instances being visible. Posterior to the upward projection of the superior surface of the postpubis is a shallow, roughened depression which was in contact with the lower anterior prolongation of the ischium. A cross section at the broken end of the postpubis of Cat. No. 4282, U.S.N.M., shows it to be subcircular in outline. The distal end is slightly expanded, especially in the ventral direction. In No. 1880, Yale Museum, holotype of *C. medius*, in which this element is complete, the postpubis is 480 mm. in length. Its distal end is 23 mm. wide in the vertical direction.

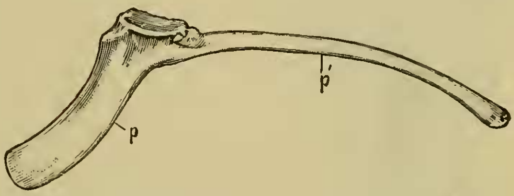


Fig. 32.—Left pubis of Camptosaurus dispar Marsh. Paratype. No. 1878, Yale Museum; $\frac{1}{12}$ nat. size. External view. *p*, pubis; *p'*, postpubis. After Marsh.

The anterior ends of the pubes do not meet medially.

THE HIND LIMB.

The hind limb and foot in *Camptosaurus* is about twice the length of the fore limb and foot and much more robust. The tibia is slightly shorter than the femur. There are four ossified elements in the tarsus, the calcaneum and astragulus being distinct.

The femur.—Unfortunately the femora are lacking in Cat. No. 4282, U.S.N.M., but in a second, larger individual both are present, and two more, representing as many individuals, were found in the collection. All are remarkably free from distortion, and in a fine state of preservation. The description to follow is based upon the femora of No. 5818 (see fig. 33).

The femur is the most robust bone of the skeleton. It has a curved shaft, and is compactly and strongly built throughout. The forward arctuation of the shaft distinguishes this bone from all other known American predentate dinosaurs excepting *Laosaurus* and *Dryosaurus*. A compressed inner or fourth trochanter (*b*, fig. 33) of the pendant type is developed on the postero-internal margin of the shaft. Dollo has called attention to this type of trochanter in *Iguanodon* as indicating a powerful caudo-femoral musculature, as in some birds. In *Camptosaurus*, however, it appears more prominently developed than is found in any of the European representatives of this group. The fourth trochanter begins to develop somewhat above the middle of the shaft, the apex being directed downward and inward toward the distal end of the bone. Just anterior to the trochanter is a shallow vertical depression with a markedly rugose surface which extends out on the internal surface of the trochanter. The head (*h*, fig. 33) is well developed and subglobular in form, and is attached by a short, thick neck at nearly a right angle to the main axis of the shaft. The articular surface of the head is somewhat rugose, and this rugosity is continued along the superior surface of the greater trochanter to its external border. A prominent lesser trochanter (*a*, fig. 33) rises on the antero-external surface of the upper part of the shaft, nearly to the height of the greater trochanter, as a transversely compressed blade. Posteriorly the lesser trochanter is separated from the shaft by a deep, narrow cleft. Behind the head is a pronounced groove separated from a second concave depression on the posterior median surface of the shaft by a heavy, rounded, longitudinal swelling. The superior surface of the greater trochanter (2, fig. 42) is wider and more gently rounded antero-posteriorly than the head. The distal end has the usual condyle shape, though the inner condyle (*c*, fig. 33) is much more robust than the outer. The two condyles are separated by a deep, intercondylar groove, wider at the bottom than the top. Both condyles project decidedly backward. The anterior intercondylar groove (2, fig. 42) is wide and of moderate depth, con-

Fig. 33.—Right femur of Camptosaurus dispar Marsh. Cat. No. 5818, U.S.N.M.; $\frac{1}{8}$ nat. size. Inner view. *a*, lesser trochanter; *b*, inner trochanter; *c*, inner condyle; *h*, head. From a photograph.

trasting strongly with the deep, narrow, almost "tunnel-shaped," anterior-intercondylar groove in *Trachodon*. The shaft of the femur appears to be somewhat twisted, due to the alteration of the aspect of its surfaces, that which at the proximal end is external becoming at the distal end anterior. There is a small roughened area on the extero-posterior angle of the distal portion of the shaft for the attachment of muscles, and just above the beginning of the inter-condylar depression or groove on the anterior surface is a second roughened patch. The outer surface of the outer condyle is decidedly concave, forming a wide, longitudinal depression at the distal end, in which a large tendon must have passed.

Measurements of Specimen, Cat. No. 5818, U.S.N.M.

	mm.
Greatest length of right femur	592
Greatest diameter of proximal end	190
Greatest diameter of distal end	178

The tibia.—The tibia in *Camptosaurus* is shorter than the femur, in which respect it may be distinguished from *Laosaurus*, *Dryosaurus*, and *Hypsilophodon foxii*. It is constricted medially, but greatly expanded at either extremity, the longer axes of the expanded ends being at nearly right angles to one another. The proximal end of the tibia shows a division of the articular surface into two condyles, which project posteriorly, separated by an inter-condylar groove, the internal one (*c*, fig. 34) being the heavier. A large enemial crest (*b*, fig. 34) projects outward from the upper end of the shaft in front of the external condyle.

Fig. 34.—Right tibia and astragulus of Camptosaurus dispar Marsh. Cat. No. 5818, U.S.N.M.; ⅙ nat. size. Inner view. *a*, astragulus; *b*, enemial crest; *c*, inner condyle. From a photograph.

The distal end is divided into two malleoli, of which the inner is the shorter and heavier, its articular surface looking downward and forward, while the external is longer and thinner and looks directly downward. These are separated on the front surface of the bone by a shallow groove. As in *Triceratops*, the outer malleolus falls below the superior border of the astragulus. Its flattened anterior surface was in contact with the distal extremity of the fibula. The posterior surface of the distal end of the tibia is angularly convex transversely.

Measurements of Specimen, Cat. No. 5818, U.S.N.M.

	mm.
Greatest length of right tibia	531
Greatest diameter of proximal end	222
Greatest diameter of distal end	90

The fibula.—The fibula of No. 1877, Yale Museum, is a slender bone, being somewhat shorter than the tibia. It has a flattened shaft above, which is subcylindrical below, with flattened expanded extremities. The face of the proximal end which was applied to the tibia is concave antero-posteriorly, while the outer surface is convex. The articular surface of this end is nearly straight antero-posteriorly, but roughened and gently rounded transversely. The expansion of the upper end takes place more especially toward the anterior border which overhangs considerably the constricted shaft. As with the tibia, planes passed through the longer axes of the expanded articular ends would cut one another at nearly right angles. Internally the distal extremity is plain and was closely applied to the opposing flattened surface of the outer anterior face of the tibia. The articular end is roughened and concave and viewed from below is semicircular in outline. The shaft has a small medullary cavity. The distal end articulates closely with the upper surface of the calcaneum.

THE HIND FOOT.

The astragulus.—The astragulus, although closely applied, was not ankylosed to the tibia, even in adult individuals. Its upper surface is the counterpart of the inner articular surface of the tibia.

The upper surface (see *a*, fig. 34) is deeply concave from front to back and divided by a ridge, which marks out two portions corresponding to the inner and part of the outer tibial malleolus. These two surfaces meet one another at an obtuse angle. The distal surface is convex antero-posteriorly, with a broad, shallow depression medially, making this surface slightly concave transversely. The anterior margin is a thickened lip. The posterior margin is stout, and viewed from above, terminates in a heavy, angular, posterior point. The inner end is comparatively thin and probably nonarticular, although a prominently developed projecting knob on the antero-internal angle appears to have been closely apposed to the distal inner surface of the fibula. The anterior half of the external depression of the dorsal surface is nonarticular and did not come in contact with the tibia, but formed the walls of an opening leading down between this bone and the *os calcis*. The outward knob-like projection overlaps the outer surface on the distal part of the tibia. On the anterior internal surface, just below the superior border, is an elongated pit.

There is no ascending process on the astragulus of *Camptosaurus.*

Measurements of Specimen, Cat. No. 5818, U.S.N.M.

	mm.
Greatest transverse diameter	139
Greatest antero-posterior diameter	95

The calcaneum.—Seen from the outside, the calcaneum is subcrescentic in outline. The upper surface is divided by a diagonal ridge into two articular faces. The anterior one, which is above the heavier end of the bone, receives the distal end of the fibula. The posterior articular portion has its surface below the level of the fibular surface and is deeply concave antero-posteriorly, and receives the outer part of the tibial malleolus. This portion has the greatest transverse diameter. The posterior margin is rounded transversely and turns up as a thickened rounded lip. The ventral surface is convex from front to back, the inner border being in contact with the outer edge of the astragulus. The outer surface vertically is gently concave. The calcaneum is represented in two individuals in the National Museum, Cat. Nos. 5473 and 5961, also in the holotype of *C. dispar*, No. 1877, Yale Museum, which, being the most complete element, furnished the following measurements:

Measurements of Specimen, No. 1877, Yale Museum.

	mm.
Greatest extent antero-posteriorly of calcaneum	87
Greatest extent transversely of calcaneum	55

Distal tarsals.—The distal row of tarsals (see *t*, fig. 35) in *Camptosaurus* consists of two flattened, cushion-like bones, which remain distinct, never fused with the metatarsals, as Hulke has suggested in *Iguanodon*, and whose separateness would be restricted to the embryo. The external one, viewed from above, is subtriangular in outline. Its proximal surface is shallowly cupped, the narrowed portion being directed backward. The distal articulating surface is concave antero-posteriorly and fits closely to the proximal end of Metatarsal IV, as shown in fig. 35. There are deep longitudinal pit-like depressions on the anterior and internal surfaces. Both proximal and distal articulating surfaces are smooth. The tarsal borne by Metatarsal III is an irregular elliptical shaped bone, somewhat thinner than the outer. Its distal articulating surface and all of the surrounding edges are roughened and pitted. This surface is slightly convex, while the proximal surface is gently concave and quite smooth except near the edges. In specimen, Cat. No. 4277, U.S.N.M., these elements have been retained by the matrix in their mutual relationship with the metatarsals, so there can be no question concerning their exact position. Even without this positive evidence, the conformation of their surfaces with the proximal ends of the metatarsals would have enabled one to place them accurately.

Measurements of Specimen, Cat. No. 4277, U.S.N.M.

	mm.
Greatest transverse diameter of outer tarsal	52
Greatest antero-posterior diameter of outer tarsal	72
Greatest transverse diameter of inner tarsal	64
Greatest antero-posterior diameter of inner tarsal	92

The metatarsals.—There were three functional digits in the hind foot, the first being rudimentary and the fifth wanting. The metatarsals are much longer and heavier than the metacarpals, the third being the longest. The proximal ends of the second, third, and fourth metatarsals are in the closest mutual apposition, their shafts being closely applied for about one-half of their length. The third and fourth support the two cushion-like tarsalia.

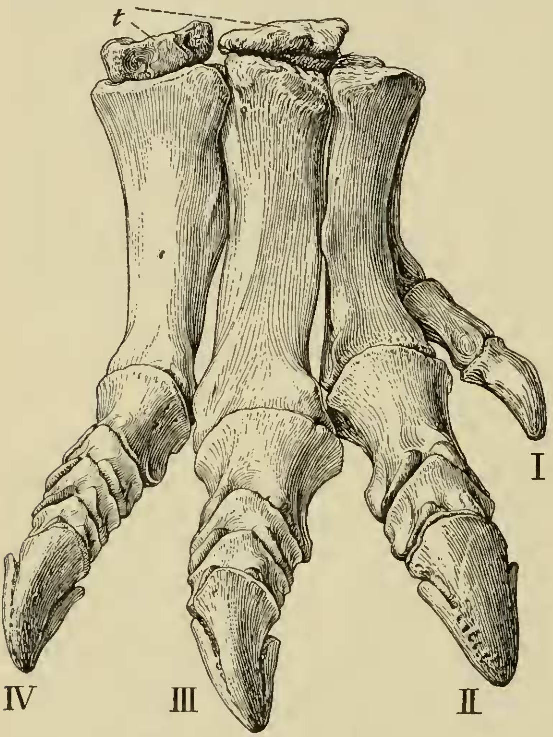


Fig. 35.—Right hind foot, Camptosaurus dispar Marsh. Cat. No. 4277, U.S.N.M.; ¼ nat. size. Seen from the front: *t*, two tarsal bones of the distal row; *I, II, III, IV*, first to fourth digits. Unguals of digits *I, III*, and *IV* drawn from the feet of other individuals.

The metatarsal of the first digit is a short, splint-like, irregularly curved bone, with a smooth, rounded proximal end compressed laterally. The thickened rugose distal articular end looks out obliquely from the main axis of the shaft, and supports two phalanges. It appears quite as Marsh has described it as being rudimentary and probably did not reach the ground. It articulates loosely with Metatarsal II, lying in a broad, shallow, longitudinal depression on the inner proximal half of this metatarsal.

The second metatarsal is slightly longer than the fourth, the third being longest. The proximal end is compressed transversely, but is much lengthened antero-posteriorly. The face which is applied to the third is plane, while the outer surface is irregularly concave. The articular end is gently convex antero-posteriorly, and has a roughly pitted surface. Just below the middle of the shaft on the antero-external border a thin lip-like process is developed which laps over and is closely applied to a roughened surface on the antero-internal border of the shaft of Metatarsal III. At this point the shaft is bent outward, which throws the distal part away from the median bone. The distal end is stout, and subquadrilateral in outline, except that it is bisected by a deep, rounded notch on the posterior border. This end is rounded antero-posteriorly. The pits for the attachment of lateral ligaments are large and fairly deep. The proximal end of the third metatarsal is roughly triangular in outline, the thickened portion being in front. The articular surface is roughened and slightly concave for the reception of the flattened tarsale of the distal row. The inner surface of the proximal half is plane, but below, this border of the shaft is rounded. Viewed anteriorly the bone remains about the same width, being slightly expanded at the distal end. Viewed laterally, however, the shaft contracts rapidly from the proximal toward the distal pulley-like articular end. The external surface of the proximal end has two oblique faces, which are opposed by the excavated internal surface of the fourth metatarsal. The pits for the attachment of lateral ligaments are large but shallow.

Seen from the proximal end the fourth metatarsal is subtriangular, the apex being directed outward. The slightly roughened articular surface in front is concave and receives the distal tarsale closely. The internal surface of the upper half is roughened and fits closely to the upper surface of the third metatarsal. The shaft is compressed antero-posteriorly and is wider than thick. As in the second metatarsal the lower half diverges outwardly and is free from the median or third metatarsal. The distal end is expanded, more especially antero-posteriorly than laterally. The distal articular end is rounded and roughened on the posterior but smooth on the anterior half. The pits for the lateral ligaments are large, the internal being shallow, the external very deep. The numbers of the phalanges, beginning with the first, are 2, 3, 4, 5, and correspond, as Hulke [a] has pointed out, to the first, second, third, and fourth toes in the foot of existing lizards and birds. *Hypsilophodon foxii* has the same formula. The proximal phalanges are rather long, with pulley-shaped distal and concave proximal ends. The phalanges have their articulating ends closely applied to one another. A median rounded vertical ridge on the proximal end fits into a corresponding depression on the proximal end of another, thus forming a strong union which would allow but little lateral motion. There are deep, well-defined lateral pits for the attachment of ligaments on most of the phalanges. The second, third, and fourth phalanges of Digit IV are considerably more shortened than the other phalanges. The ungual phalanges

[a] Phil. Trans. Roy. Soc. London, CLXXIII, 1882, p. 1053.

are long, pointed, and slightly curved longitudinally and laterally, being deflected inward. They are somewhat depressed, except the ungual of Digit I, which is higher than wide, and more sharply pointed. They were undoubtedly incased in compressed pointed claws, as indicated by a pair of lateral grooves on each ungual (see fig. 35). The ungual of the second digit is the more robust of the series.

Measurements of the right hind foot of Specimen, Cat. No. 4277, U.S.N.M.

Digits.	I.	II.	III.	IV.
	mm.	*mm.*	*mm.*	*mm.*
Greatest length of metatarsals	133	212	234	202
Greatest antero-posterior diameter proximal end of metatarsals	15	118	106	77
Greatest transverse diameter of proximal end of metatarsals	6	55	66	81
Greatest transverse diameter of distal end of metatarsals	26	64	76	45
Greatest length 1st row phalanges	58	95	85	63
Greatest length 2d row phalanges	[a] 59	69	53	39
Greasest length 3d row phalanges	....	94	43	30
Greatest length 4th row phalanges	....	....	[a] 90	29
Greatest length 5th row phalanges	....	....	....	[a] 81

[a] Measurements from other individuals of about same proportions as No. 4277.

THE GENUS CAMPTOSAURUS.

In a paper published in December, 1879,[a] Prof. O. C. Marsh proposed the genus *Camptonotus*, and at the same time described two species, *C. dispar* and *C. amplus*, both from the Morrison beds (Atlantosaurus beds of Marsh) of the Upper Jurassic. In the same article he proposed the family Laosauridæ to include the two genera *Laosaurus* and *Camptonotus*.

In 1881,[b] without comment, he proposed the family Camptonotidæ, under which the following genera were included: *Camptonotus*, *Laosaurus*, *Nanosaurus*, and *Diracodon*. In 1882 [c] he briefly defined the family, including in it the European genus *Hypsilophodon*, *Diracodon* being removed to the Stegosauridæ.

The name *Camptosaurus* was proposed by Marsh in 1885 [d] to replace *Camptonotus*, preoccupied.

Dollo,[e] in 1888, gave an emended definition of the family, using the older term Camptonotidæ, under which he placed the two genera *Camptonotus* and *Hypsilophodon*. To distinguish the former from the latter, "*Camptonotus*" is defined as follows: "Two phalanges in manus-digit-V. Preacetabular process of the ilium slight. No rudiment of pes-digit-V."

In 1889, Lydekker [f] referred three species to the genus *Camptosaurus*, *C. leedsi*, *C. valdensis*, and *C. prestwichii*. Seely's genus

[a] Amer. Journ. Sci., XVIII, 1879, pp. 501–503.

[b] Idem, XXI, 1881, p. 423.

[c] Idem, XXIII, 1882, p. 84.

[d] Idem, XXIX, 1885, p. 169.

[e] Compt. rend. Acad. Paris, CVI, 1888, pp. 775–777.

[f] Quart. Journ. Geol. Soc. London, XLV, 1889, pp. 47, 48.

Cumnoria being considered a synonym. In 1890[a] he characterized the genus as follows:

Teeth simpler than in the typical group of *Iguanodon*. Cervical vertebræ opisthocoelous; sacrals flattened inferiorly and not anchylosed; manus with five normal digits. Ilium typically deep with short and pointed pre- and postacetabular processes, the latter having a distinct ventral plate; pubis relatively stout and long as ischium. Femur slightly longer than tibia, with curved shaft and pendant inner trochanter; typically four functional digits in pes.

In 1894,[b] Marsh published a restoration of the skeleton of *Camptosaurus dispar*, and additional characters relating to the osteological structure were noted. Four months later,[c] he briefly described the two species, *C. medius* and *C. nanus*, and at the same time characterized the genus as follows:

Premaxillaries edentulous with horny beak. Teeth large, irregular, and few in number. A supra-orbital fossa. Cervical vertebræ long and opisthocoelous. Lumbars present. Five free vertebræ in sacrum, with peg-and-notch articulation. Limb bones hollow. Fore limbs small. Sternum unossified. Five functional digits in manus. Prepubis long and broad, postpubis elongated. Femur longer than tibia. Metatarsals short. Three functional digits in pes: the first rudimentary and the fifth wanting.

In 1895[d] Marsh redefined the family Camptosauridæ, retaining in it only the genus *Camptosaurus*, the other genera being removed to separate families proposed for them. This definition was repeated, with a few additions, in 1896, in his "Dinosaurs of North America."[e]

In 1899, Nopcsa[f] gives a brief preliminary description of a new species, *C. inkeyi*, from the Cretaceous of Hungary, and in 1901[g] placed the genus under the subfamily Camptosauridæ.

In 1902, Hay[h] included under the family Camptosauridæ[i] the

[a] Cat. Fossil Reptilia and Amphibia in Brit. Mus., Suppl. to Pt. 4, 1890, p. 259.

[b] Amer. Journ. Sci., XLVII, 1894, pp. 245, 246, pl. VI.

[c] Idem, XLVIII, 1894, pp. 85, 88.

[d] Idem, L, 1895, p. 497.

[e] 16th Ann. Rept. U. S. Geol. Surv., Pt. 1, 1896, p. 243.

[f] Denk. k. Akad. Wien, LXVIII, 1899 (1900), p. 579.

[g] Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

[h] Bull. No. 179, U. S. Geol. Surv., 1902, p. 501.

[i] Laosauridæ Marsh has priority over Camptosauridæ Marsh, and if *Laosaurus* is to be included in the same family with *Camptosaurus*, the former name should be retained. On the other hand, if the two forms represent distinct families, as originally proposed by Marsh, Camptosauridæ is represented by the genus *Camptosaurus*, and Laosauridæ by the genera *Laosaurus* and *Dryosaurus*. The superfamily Iguanodontidea proposed by Hay in his Bibliography and Catalogue of the Fossil Vertebrata of North America (p. 500), should then include the families Camptosauridæ, Laosauridæ, Nanosauridæ, Trachodontidæ, and the European Iguanodontidæ and Hypsilophodontidæ. For obvious reasons, *Thespesius* Leidy should be removed from the Iguanodontidæ to the Trachodontidæ.

genera *Camptosaurus Laosaurus*, and *Dryosaurus*, *Nanosaurus* being retained under the family Nanosauridæ as originally proposed by Marsh.

In the same year, Zittel[a] defines the genus *Camptosaurus* thus:

Attaining a total length of about 10 m. Cervical ribs short; dorsal vertebræ amphiplatan; sacrals not anchylosed. Pubis robust, postpubis of equal length with the long and slender ischium. Pendant inner fourth trochanter of femur marked. Proximal tarsals separated.

As shown by a recent study of the typical specimens in conjunction with all other available material, it is found that the earlier definitions of the genus, as briefly reviewed above, are in some respects in error. Such inaccuracies as have been detected can, in most instances, be attributed to the incompleteness of the material at the command of the earlier authors.

The characters displayed by the discovery of new material, combined with a restudy of the typical specimens, show that the genus *Camptosaurus* may now be characterized as follows:

Generic characters.—Premaxillaries edentulous, with horny beak. Teeth large, irregular and comparatively few in number. A supraorbital fossa. Cervical vertebræ posterior to the third opisthocoelous manus with five digits, metacarpal of first digit ankylosed with radiale. Ilium with long preacetabular process. Pubis well developed, with broad anterior blade, postpubis elongated reaching end of ischium. Ischium with long shaft terminated by an expanded hammer-like end. Femur curved, longer than tibia, with pendant inner trochanter extending on to the distal half of the shaft. Astragulus and calcaneum free, former without ascending process. Pes robust with four digits, first being rudimentary.

Camptosaurus dispar is the type-species of the genus, and, as will be discussed later, was founded on the remains of at least two and maybe three individuals, all from the Jurassic, Quarry No. 13, near Como, Albany County, Wyoming. Eight species have been described as pertaining to this genus, of which four are American and four European. An alphabetical list of the species assigned to the genus is given below.

ALPHABETICAL LIST OF SPECIES.[b]

Camptosaurus amplus Marsh. (No. 1879, Yale University Museum.)

Camptosaurus browni, new species. (Cat. No. 4282, U.S.N.M.)

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[a] Text-book of Paleontology, English Translation, II, 1902, p. 238.

[b] In Földtani Közlöny, Budapest, XXXI, 1901, p. 210, Nopcsa inadverently includes *Dryosaurus altus* (Marsh) in a list of the described species of *Camptosaurus*. Marsh first described this form as *Laosaurus altus* and later referred it to *Dryosaurus*. While it represents a closely related genus, it is quite distinct from *Camptosaurus*.

Camptosaurus depressus, new species. (Cat. No. 4753, U.S.N.M.)

Camptosaurus dispar Marsh. (No. 1877, Yale University Museum.)

Camptosaurus inkeyi Nopcsa. (Location of type unknown.)

Camptosaurus leedsi Lydekker. (Coll. of A. N. Leeds, Eyebury, England.)

Camptosaurus medius Marsh. (No. 1880, Yale University Museum.)

Camptosaurus nanus Marsh. (Cat. No. 2210, U.S.N.M.)

Camptosaurus prestwichii Lydekker. (Museum in Oxford, England.)

Camptosaurus valdensis Lydekker. (No. R167, British Museum.)

SYSTEMATIC DESCRIPTION AND REVISION OF SPECIES.

In the description and revision of the various species to follow, Hatcher's method of treatment in his monograph on the Ceratopsia is adopted, with modifications. A reference to the original description of each will first be given, followed by references to the more important literature which further elucidates the species under consideration. These references will be arranged in chronological order.

When possible, the parts constituting the type will be listed and definitely located, also the name of the museum to which each belongs, as well as the distinctive catalogue numbers which have been assigned to them. The locality and geological horizon from which the specimen came, and the name of the collector, when known, will be given, so that in each instance a permanent record of the character and location of the type material will hereafter be available.

In the discussion of the species, the original description of each will first be quoted, followed by a further description of such parts of the skeleton as considered not sufficiently elucidated in the original text, and a presentation of my own views. In conclusion an attempt will be made to give a brief characterization of each valid species.

CAMPTOSAURUS DISPAR Marsh.

Camptonotus dispar Marsh, Amer. Journ. Sci. (3), XVIII, 1879, pp. 501–503, pl. III.

Camptosaurus dispar Marsh, Amer. Journ. Sci. (3), XXIX, 1885, p. 169.

Camptosaurus dispar Lydekker, R. Cat. foss. Reptilia and Amphibia Brit. Mus., Pt. 1, 1888, p. 192, fig. 36.

Camptosaurus dispar Marsh, Amer. Journ. Sci. (3), XLIV, 1892, p. 176, pl. v; XLVII, 1894, pp. 245–246, pl. vi; XLVIII, 1894, p. 85, pl. v, fig. 1; Geol. Mag., Dec. 3, I, 1894, pp. 193–195, pl. vi; 16th Ann. Rept. U. S. Geol. Surv. 1894–95, Pt. 1, 1896, p. 196, pls. LIV, LVI; Compt. rend., 3 me Congrès International de Zoologie, Leyden, 1896, pp. 196–211, fig. 7; Mon. U. S. Geol. Surv., XXVII, 1897, p. 502, pl. XXIII; Amer. Journ. Sci. (4), VII, 1899, p. 232, fig. 2.

Cumnora (*Camptosaurus*) *dispar* WILLISTON, Amer. Nat., XXIV, 1890, p. 472.

Camptosaurus dispar ZITTEL, Handbuch der Paleontologie, I, 1890, p. 756, fig. 666.

Camptosaurus dispar FÜRBRINGER, Jenaische Zeitschr. f. Naturwiss., Jena, XXXIV, 1900, p. 350.

Camptosaurus dispar NOPCSA, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Camptosaurus dispar HAY, Bull. No. 179, U. S. Geol. Surv., 1902, p. 501.

Holotype.—No. 1877 consists of the atlas, axis, seven cervicals, first dorsal, left scapula (lacking upper half of the blade), left coracoid (also incomplete), two femora, tibia, fibula, astragulus, calcaneum, nearly complete pes, and two manus.

Paratype.—No. 1877*a*, so far as I am able to determine, consists of a sacro-dorsal and four sacral vertebræ, all united by suture.

Paratype.—No. 1878 consists of the left ilium, pubis, and ischium, figured in the original description, together with a humerus, radius, and ulna.

The description calls for teeth and part at least of the lower jaws. It may be Marsh refers here to a pair of incomplete jaws, No. 1888, in the same collection, but this can not now be absolutely determined.

The above specimens were all collected by Mr. W. H. Reed from Quarry No. 13, Jurassic (Morrison beds), 8 miles east of Como, Wyoming, and are now preserved in the collection of the Yale University Museum.

The original description is as follows:

The present genus is most nearly allied to *Laosaurus*, but differs in several points. The cervical vertebræ are all opisthocoelous, while those known in *Laosaurus* are nearly plane. The pubis, moreover, is broad and thin in front of the acetabulum, and directed well forward. It has a deep, well-marked articular face for the support of the femur. The ischium is expanded at its distal end, and has an extensive surface for union with its fellow. The femur is longer than the tibia.

This genus agrees with *Laosaurus* in one important character, namely, the sacral vertebræ are not coossified. That this is not merely a character of immaturity is shown by some of the other vertebræ in the type specimen, which have their neural arches so completely united to the centra that the suture is nearly or quite obliterated. To this character of the sacral vertebræ the name of the present genus refers. With *Laosaurus* this genus forms a distinct family, which may be called *Laosauridæ*.

The teeth in *Camptonotus* resemble those of *Laosaurus*, and are in a single row in close-set sockets. The rami of the lower jaws were united in front only by cartilage. There are nine cervical vertebræ, all of which bear short ribs, as in the Crocodiles. The dorsal vertebræ have their articular faces nearly plane. The sacral vertebræ in all the known specimens are separate, and their transverse processes are each supported by two centra. The chevrons have their articular faces joined together.

The fore limb is much reduced in size. There are five digits in the manus, supported by nine carpal bones, three of which are united in one on the radial side. The number of phalanges, beginning with the first digit, was 2, 3, 3, 3, 2.

The form and proportion of the various elements of the fore limb are shown in Plate III, fig. 1.

The pelvic arch is quite unlike any hitherto described. In its general form the ilium resembles that of *Morosaurus*, but the proportions are reversed. The massive portion in the present genus is not in front, but behind, as the ischium is larger than the pubis. The relative position and form of the elements of the pelvic arch are shown in the figure below.

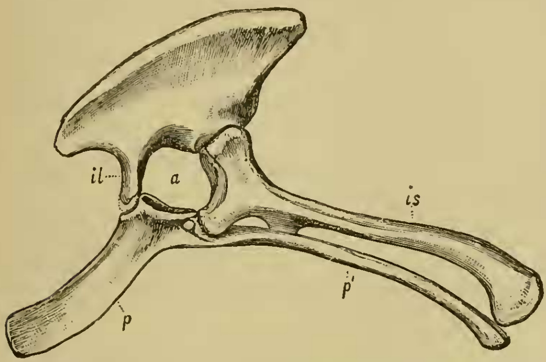

FIG 36.—PELVIC ARCH OF CAMPTOSAURUS (CAMPTONOTUS) DISPAR MARSH. NO. 1878, YALE MUSEUM; SIDE VIEW; $\frac{1}{12}$ NAT. SIZE. *a*, ACETABULUM; *il.*, ILIUM; *is.*, ISCHIUM; *p*, PUBIS; *p'* POSTPUBIS. AFTER MARSH.

The femur has a long pendant third trochanter, and a prominent ridge to play between the tibia and fibula. The tibia is stout, and somewhat shorter than the femur. The fibula is slender, and shorter than the tibia. The astragulus and calcaneum are distinct. The second row of tarsals contains but two bones. The first digit in the pes was rudimentary, and did not reach the ground. The second, third, and fourth were well developed. The fifth was entirely wanting. The number of phalanges, beginning with the first digit, was 2, 3, 4, 5. The structure of the hind limb and foot is well shown in Plate III, fig. 2, which is taken from the same skeleton as fig. 1.

Some of the principal measurements of the present species are as follows:

	mm.
United length of the nine cervical vertebræ	565
Length of axis	54
Transverse diameter of posterior articular face	41
Length of ninth cervical vertebra	64
Transverse diameter of posterior articular face	63
Length of humerus	337
Length of radius	245
Length of ulna	260
Length of femur	565
Length of tibia	555

The known remains of this species indicate an animal about 8 or 10 feet in height and herbivorous in habit. All the specimens discovered are from the Atlantosaurus beds of the Upper Jurassic.

Concerning the status of the material upon which the above genus and species was founded, Dr. R. S. Lull writes me as follows: "I find an old manuscript sheet in Marsh's writing in which No. 1877 is called the "type" of *C. dispar*. Professor Schuchert and I have decided therefore that 1877 should be the holotype and 1878 the paratype." No. 1877*a* may pertain to the holotype, but, as shown later, appears to represent a distinct individual.

While Marsh in the above description brings out most of the essential characteristics of this form, a recent examination of the type specimen, combined with a study of additional material, shows that several of the observations made at that time are not substantiated. These remarks apply particularly to the description and figures of the scapula and ilium, the latter, as will be shown later, being one of the most characteristic elements of the skeleton.

In a note published in the American Naturalist,[a] Dr. S. W. Williston first called attention to the perpetuation of an error by Mr. Richard Lydekker, who was struck with the great resemblance between the ilia (excepting the preacetabular portion) of *Camptosaurus dispar* and *Iguanodon dawsoni*. Doctor Williston says:

> The fact is that the figure of the former is wrong. The anterior portion of the ilium of the type had been broken off and weathered, indications of which are distinctly seen in the specimen. Professor Marsh had this demonstrated to him more than five years ago, and there are other ilia in the Yale Museum in which this process is complete.

I quite agree with Doctor Williston's observations with the exception that none of the ilia in the Yale Museum, so far as I could find, show the complete preacetabular process, but there are other specimens in the collection which have considerably more of the process preserved than is shown in the ilium figured. That Marsh clearly recognized the incorrectness of his first figure is evident, since in a later paper[b] he republished a figure of the pelvic bones of *C. dispar* to the ilium of which had been added in outline a long, sharply-pointed anterior process. That he was still in error is clearly shown by the left ilium of *C. dispar*, Cat. No. 5473, U.S.N.M., which is terminated anteriorly by a somewhat rounded spatulate end (see fig. 29).

The incomplete scapula of the holotype was correctly figured on Plate 3, fig. 1, in the original description, but later[c] the scapula and coracoid are represented as being complete. I am at a loss to understand, however, upon what evidence Marsh based this restoration of the upper free extremity of the scapula, which is so entirely different from all other scapulæ pertaining to the members of this genus. None of the ten or more scapulæ examined by me show anterior expansion of this end, but all agree, with slight variations, in having the same general contour as the scapula of No. 4282, seen in fig. 23. I dwell on the correctness of the contour of the type of *C. dispar*, from the fact that the specific characterization of *C. nanus* (see fig. 40) given by Marsh was based primarily upon the differences in contour displayed by the scapulæ of the two specimens discussed here.

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[a] Amer. Nat., XXIV, 1890, pp. 472–473.

[b] Amer. Journ. Sci., XLIV, 1892, pl. v.

[c] Idem, XLVIII, 1894, pl. v.

Detailed description.—The skull and jaws of the holotype are unknown, and the complete neck with the first dorsal is all that is preserved of the vertebral column of this individual. The cervicals, posterior to the third, are all opisthocoelous, the second and third, as in the other species of the genus, being plano-concave. The median ventral keel is wider and heavier, and the centra are not so deeply excavated laterally as in *C. browni*. The cervical region of the holotype of *C. medius* being still inclosed by the matrix, direct comparisons with that species could not be made.

The first dorsal, as in *C. browni*, is opisthocoelous and shows the same transition of the parapophysis from the anterior end of the centrum in the ninth cervical to a position well up on the side of the neural arch on this vertebra. It is the first vertebra of the series to bear a true spinous process—a short spine 11 mm. high, slightly thickened and roughened at its upper extremity. The neuro-central sutures are plainly shown on all of the vertebræ preserved.

The sacrum, No. 1877*a*, Yale University Museum (see Plate 13), although considered by Marsh as pertaining to the holotype, in all probability belongs to another individual. This is shown by a comparison of the measurements of the cervical and sacral vertebræ with the homologous parts of Cat. No. 4282, U.S.N.M., the proper association of the different elements of this skeleton being unquestionable. Referring to the table of measurements on page 243, it will be seen that the cervicals are smaller and the sacrals larger than those of No. 4282. On account of the difference in proportions noted, I am inclined to believe the sacrum represents a distinct individual, and should, therefore, as it was included in the material first described, be considered a paratype, to which the catalogue number 1877*a* has been given to distinguish it from the holotype, No. 1877.

In the sacral region of No. 1877*a* there are five vertebræ united by suture, of which the posterior four represent true sacrals, or those which give support to sacral ribs. This interpretation excludes the anterior vertebra of the series which may be regarded as sacro-dorsal (*a*, Plate 13), as shown by the weak diapophyses which carried a single-headed rib. Marsh has described the peculiar peg-and-notch articulation (see 3, fig. 37) of the centra of this region and makes it an important feature of the genus, but after a study of several sacra I am inclined to believe too much stress has been laid on this character, as it appears to be a variable one. For example, in the sacrum of *C. browni* this peculiarity is only weakly developed between S_3 and S_4 (see fig. 17), and in *C. nanus* there is only the suggestion of such an articulation. In the sacrals under discussion this articulation is faintly shown between S_1 and S_2, more pronounced between S_2 and S_3, and strongly developed between S_3 and

S_4 (see fig. 37). The ventral surfaces of all the centra are flattened, with a slight, median, longitudinal depression, which at once distinguishes them from the keeled or hæmally rounded sacral centra of *C. browni.* The ventral surface of the sacro-dorsal is regularly and evenly rounded and is without the decided keel present in that of *C. browni.*

The two spinous processes preserved (see Plate 13) rise as thickened plate-like spines, the upper termination being thickened transversely, especially on the anterior part of this end. The spine of the sacro-dorsal is heavier anteriorly than the spine of sacral one, and probably indicates the culmination in the development of the spinous processes. The border below the thickened termination is compressed and presents a sharp anterior edge. The posterior border is somewhat thickened and has a shallow, vertical groove which may have received the sharp anterior edge of the spine posterior to

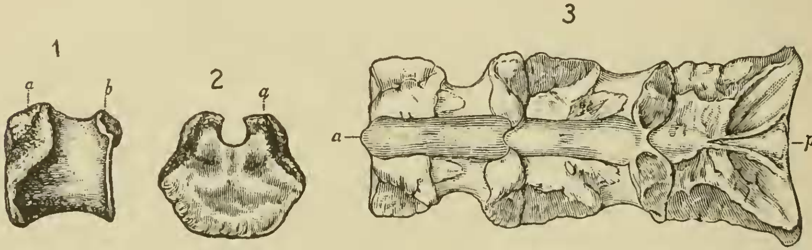


Fig. 37.—(1) Lateral and (2) front views of first sacral centrum Camptosaurus dispar Marsh. No. 1877*a*, Yale Museum. Paratype. 1/6 nat. size. *a*, anterior face for articulation of first sacral rib; *b*, posterior articulating surface for second sacral rib. (3) Posterior sacral vertebræ of same. 1/4 nat. size. Showing peg-and-notch articulation; top view: *a*, anterior end; *p*, posterior end. After Marsh.

it, which would give the plate-like appearance of the three median sacral spines, as shown by Marsh in his first restoraton of *C. dispar.*

In No. 1878, Yale Museum, the ilium, pubis, and ischium are preserved, the two former elements being incomplete, that is, the ilium lacks most of the preacetabular and postacetabular processes, and the pubis most of the post-pubis, which, as shown in Plate 15, reproduced from a photograph of the specimens, has been restored in plaster.

In the pelvic bones are found the chief differences which serve to separate this species from the other members of the genus. The ilium, in proportion to its length, is considerably deeper and more robust than in any of the other species (compare figs. 29 and 30). The preacetabular notch is wide and the acetabular notch deep. The oblique border of the supero-posterior end is much longer—in most individuals a third longer than in *C. browni*—and terminates posteriorly as a thickened angular end.

The preacetabular process of this particular individual is unknown, and in the first figure of this element it was represented as being a very short, blunt process (see fig. 36). As previously stated, the first figures given are now known to be erroneous.

The shaft of the ischium of *C. dispar* is more robust, and at its distal termination has a larger hammer-like development of this end than is found in any of the known species (compare *is*, Plates 15 and 16), the greatest diameter being 106 mm. The pubis does not show any especial differences, while the post-pubis is almost wholly restored.

The limb and foot bones do not exhibit any especial characters except a more robust development than is found in the smaller species. It is at once distinguished from *C. amplus* by the greater size and the compressed, sauropod-like ungual of Digit I of the latter, as compared with the rounded, claw-like element of *C. dispar* (compare fig. 35 with fig. 38 and Plate 17).

Of the pes of No. 1877 I need mention only the extreme shortness of Metacarpal I as figured by Marsh. When compared with complete elements it appears that the upper third is missing, which would account for the extreme brevity of this digit as originally figured. In the same cut Digit III is represented as bearing the heaviest ungual, when, as shown by the pes of Cat. No. 4277, U.S.N.M. (see fig. 35), Digit II carries the most robust terminal phalanx of the hind foot. A cast of the foot in question now before me shows an ungual attached to the second digit whose small articular surface indicates at once that it has been wrongly placed, and in all probability pertains to Digit IV.

The manus, if correctly associated with the pes just discussed as pertaining to the same individual, shows variation from the same elements in Cat. No. 5473, U.S.N.M., being much lighter in construction, the hind feet having about the same dimensions. The association of the fore and hind feet of this latter individual is undoubtedly correct.

The fifth metacarpal is unusually short. The ungual of Digit III is very small, weak, and sharply pointed. Carpale five, as shown in the earlier figures of the manus of *C. dispar*, contributes to the articulating surface for the ulna and is so shown in the cast of the right fore foot. The unusual position of this element would hardly point to the true interpretation of the proper articulation of these bones, and it has been depicted otherwise, as shown in fig. 28. In the right foot I can only recognize seven carpal elements, although the eighth is probably fused with the radiale and Metacarpal I, and has thus lost its identity. Carpale three is almost wholly articulated with the proximal end of Metacarpal III. It is wedge-shaped, the thickened part being posterior. Carpale two occupies a posterior position on Metacarpal II and is not visible from the front view as in the foot of Cat. No. 4277, U.S.N.M. (see fig. 28). In other respects the foot does not differ materially from the description already given in that part of the present paper devoted to the osteology of *Camptosaurus*.

The restoration (see Plate 18) of *Camptosaurus dispar* published by Marsh [a] was based on the typical specimens, and while it depicts well the general appearance of the animal, it is now known to be erroneous in the following particulars: The thoracic region is too long by at least three, and possibly five, vertebræ; all of the presacral vertebræ are rib-bearing, and thus there are no true lumbars; the anterior caudal vertebræ, as shown in the restoration, have the arches and transverse processes too high above the centra, the latter, as shown in fig. 18, being below the level of the pre- and postzygapophyses. The spines should also be more inclined backward and decrease more rapidly in height posteriorly; the transverse processes are continued too far posteriorly, as shown by two specimens in the National Museum, where they end on either the twelfth or thirteenth from the sacrum. Other minor corrections have been touched upon in the previous pages, so need no mention here.

As shown by the skeleton, *C. dispar* is an animal of quite robust proportions, only exceeded in size by *C. amplus*. Marsh estimated its length as being 20 feet.

After a review of the typical specimens as compared with the other species of the genus, *C. dispar* may now be distinguished by the following characters:

Specific characters.—Typically of large size. Cervical centra with heavy keel. Four sacrals with peg-and-notch articulation. Sacral centra flattened inferiorly. Sacro-dorsal without ventral keel. Ilium deep, and heavy in its proportions. Ischium stout, with greatly enlarged distal extremity. Ungual of Digit I of pes rounded and pointed.

CAMPTOSAURUS AMPLUS Marsh.

Camptonotus amplus MARSH, Amer. Journ. Sci. (3), XVIII, 1879, p. 503.

Camptosaurus amplus MARSH, Amer. Journ. Sci. (3), XXIX, 1885, p. 169; 16th Ann. Rep. U. S. Geol. Surv., 1894–95, Pt. 1, 1896, p. 196.

Camptosaurus amplus NOPCSA, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Camptosaurus amplus HAY, Bull. No. 179, U. S. Geol. Surv., 1902, p. 501.

Holotype.—No. 1879, Yale University Museum, was collected by Mr. Arthur Lakes from "Big Canyon Quarry," Jurassic (Morrison Beds), in the vicinity of Como, Albany County, Wyoming. It consists of a right pes nearly entire. The first description is as follows:

A second species of this genus, about three times as large as the one [*C. dispar*] just described, is represented by various remains, among which is a left

[a] Amer. Journ. Sci., XLVII, 1894, pl. VI.

hind foot nearly entire. There were three functional digits in this foot, the first being rudimentary and the fifth entirely wanting. The metatarsal of the first digit is a splint, much curved, and with the apex above. The terminal phalanx of this digit is much compressed, not round as in the smaller species. The second metatarsal is of much greater length. The terminal phalanx of this digit is longer in proportion than that of the preceding species. The third and fourth digits were large and powerful. The main dimensions of this foot are as follows:

	mm.
Length of second metatarsal	295
Greatest diameter of proximal end	113
Length of third metatarsal	345
Greatest diameter of proximal end	150
Transverse diameter of distal end	102
Length of fourth metatarsal	305
Length of first phalanx of third digit	140
Length of first phalanx of second digit	120

The remains of the present species are from a lower horizon in the Jurassic than those described above, but within the limits of the Atlantosaurus beds.

An examination of the type specimen shows it to be a right instead of a left hind foot, as originally described, and it has been so remounted, as shown in Plate 17, reproduced here from a photograph.

As Marsh has already pointed out, *C. amplus* may be distinguished from the other species of the genus, (1) by its great size, (2) by the compressed terminal phalanx of the first digit. This phalanx, in nearly all of its details, resembles the ungual of the third digit of the pes in the opisthocœlian dinosaurs, as shown in fig. 38.

Fig. 38.—Ungual of first digit, Camptosaurus amplus Marsh. No. 1879, Yale Museum. Holotype. ½ nat. size. *a*, articular end. Rough outline sketch showing its sauropod-like shape.

A second specimen, No. 1887, Yale Museum, consisting of portions of the skull and lower jaws (see Plates 7, 8, and 9), may, on account of its large size, be provisionally referred to this species. It was collected by Prof. O. C. Marsh from deposits in the Garden of the Gods, Colorado Springs, Colorado, in 1886. With this specimen was found the following note in Professor Marsh's handwriting: "Part of this animal and various Sauropoda bones were taken out by Professor Kerr in 1878." Diligent inquiry has failed to locate the repository of the parts of this specimen collected by Professor Kerr, but their association with Sauropoda remains would indicate the Jurassic age of the deposits in which they were originally found.

On page 1159 of volume 2 of Nicholson and Lydekker's Manual of Paleontology, they remark: "It is not improbable that the large Iguanodont from the Upper Jurassic of the United States, described as 'Camptosaurus amplus,' should be referred to this group of *Iguanodon*, since it has but three functional digits in the pes."

While the first digit in *C. amplus* is undoubtedly rudimentary, still it is at once distinguished from the remnant of the first metatarsal in *Iguanodon* by the heavy articular distal end of Metatarsal I, and the presence of two distal phalanges. The distal row of tarsals, as in *C. dispar*, consists of two elements (see Plate 17), although, comparatively speaking, somewhat reduced in size.

Principal measurements of Specimen, No. 1879, Yale Museum.

Digits.	I.	II.	III.	IV.
Greatest length of metatarsals	(a)	305	345	295
Greatest length of first row phalanges	66	117	124	84
Greatest length of second row phalanges	43	92	87	69
Greatest length of third row phalanges		103	60	44
Greatest length of fourth row phalanges			(b)	32

[a] Incomplete. [b] Missing.

CAMPTOSAURUS MEDIUS Marsh.

Camptosaurus medius MARSH, Amer. Journ. Sci. (3), XLVIII, 1894, p. 85, pl. IV; 16th Ann. Rep. U. S. Geol. Surv., 1894–95, Pt. 1, 1896, p. 196, pl. LIII; Mon. Geol. Surv., XXVII, 1897, p. 502, text figs. 58, 59.

Camptosaurus medius NOPCSA, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Camptosaurus medius HAY, Bull. No. 179, U. S. Geol. Surv., 1902, p. 501.

Holotype—No. 1880, Yale University Museum. This specimen was collected by Mr. W. H. Reed from "Quarry 13" in the Jurassic (Morrison beds) of Albany County, Wyoming.[a] It consists of a well-preserved disarticulated skull and jaws; 59 or more vertebræ, representing all parts of the vertebral column, of which at least half have the arches and spinous processes complete; two humeri, two ulnæ, one radius, one femur, tibia and fibula, astragulus, calcaneum, left pes, two ilia, ischium, pubis, numerous ribs, and ossified tendons.

The species was never properly defined by Marsh, the original description consisting of the few lines which follow:

> There are at least two small species of the genus (*C. medius* and *C. nanus*, noticed below). * * * *C. medius* was about fifteen feet long. * * * The skull, brain, and teeth of *C. medius* are shown on Pl. IV.

It is now known that the skull as figured[b] was reconstructed, not from the disarticulated elements of the holotype alone, but the nasal region and the lower posterior section of the skull and mandible were drawn from No. 1887, Yale Museum (see Plates 7 and 8), a very much larger individual which undoubtedly pertains to a distinct

[a] In his Bibliography and Catalogue of Fossil Vertebrata of North America Hay cites the occurrence of this species in Colorado. So far as known, it has not been found outside of Wyoming.

[b] 16th Ann. Rep. U. S. Geol. Surv., 1894–95, Pt. 1, 1896, pl. LIII.

species, as stated on page 277. Taking into consideration these facts in connection with many inconsistencies discovered in the figures, I do not believe that the skull, as illustrated, should be considered typical of the species. The teeth, as shown in fig. 9, are of the holotype, but I am unable to find that they show any distinctive characters. While the skull may show specific differences when the crania of the other forms are known, such comparisons can not be made at present, owing to the lack of material.

The parts of the type-specimen, as enumerated above, represent a considerable portion of the entire skeleton, and it is unfortunate that they have not yet been made ready for study. At present only the disarticulated elements of the skull and jaws, limb, foot, and pelvic bones (see Plate 16) have been freed from the matrix, the other parts being still largely enveloped in the hard, concretionary mass in which they were originally entombed.

Even though Marsh failed to define this form, I believe it to represent a valid species intermediate in structure between *C. dispar* and *C. browni*. From *C. dispar* (compare Plates 15 and 16), its nearest ally, it may be distinguished by the lighter structure of the pelvic bones, that is, the ilium is considerably narrower in proportion to its length. The oblique border of the supero-posterior end is somewhat shorter. The ischium is much more slender, and the hammer-like expansion of the free end less robust, its greatest diameter measuring 73 mm. Throughout the skeleton of *C. medius* appears to be lighter and more delicately constructed. The femur pertaining to the type-specimen is proportionately very short, but I am inclined to the opinion that this is either due to severe crushing, or the preparator, in joining the two ends, has omitted a section of the shaft of the bone, which would account for the extreme brevity of this element.

Except in its smaller size, the hind foot shows no essential differences when compared with that of *C. dispar*. The following are the measurements of the left pes of No. 1880:

	mm.
Greatest length of metatarsal I	74
Greatest length of metatarsal II	148
Greatest length of metatarsal III	181
Greatest length of metatarsal IV	151

It is anticipated that upon the complete preparation of the type material, characters will be disclosed by which this species may be more completely defined, but for the present it must rest on those shown by the pelvis, although the dissimilarity shown by these bones certainly suggests other and even more important differences in the other portions of the skeleton.

CAMPTOSAURUS NANUS Marsh.

Camptosaurus nanus Marsh, Amer. Journ. Sci. (3), XLVIII, 1894, p. 85, pl. v., fig. 3; 16th Ann. Rep. U. S. Geol. Surv., 1894–95, Pt. 1, 1896, p. 196, pl. LV, fig. 2.

Camptosaurus nanus Walcott, Science (2), XI, 1900, p. 23.

Camptosaurus nanus Nopcsa, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Camptosaurus nanus Hay, Bull. No. 179, U. S. Geol. Surv., 1902, p. 501.

Holotype.—Cat. No. 2210 U.S.N.M.[a] was collected by Mr. W. H. Reed from the upper Jurassic (Morrison beds), "quarry 13," near Como, Albany County, Wyoming,[b] in 1882.

The elements preserved are as follows: Portion of atlas, axis, 7 cervical, 16 dorsal, 4 sacral, and 34 caudal vertebræ, numerous cervical and thoracic ribs, right fore limb (scapula, coracoid, humerus, radius, and ulna), 2 femora, 2 tibiæ, left fibula, 2 ilia, 2 ischia, portion of left pubis, 2 metacarpals, 1 carpal, and parts of ossified tendons.

The original description is as follows:

> The smallest species of the genus *C. nanus* was not more than 6 feet in length, and perhaps 4 feet in height when standing at rest. One of the striking features of this diminutive species is its long sigmoid scapula, shown in fig. 3, Plate V. This is in strong contrast with the short, straight scapula of *C. dispar*, seen on the same plate, fig. 2.

Detailed description.—The cervical vertebræ of the present species, as compared with the corresponding parts of the larger forms, show no particular distinguishing characters, although they differ in minor details.

The entire neck and the first two dorsals remain articulated, and thus the true relationship of these parts is accurately displayed. The neck shows the same graceful upward curve of the cervicals as is found in the related species. The transition of the parapophyses from the anterior lateral border of the centrum of the ninth cervical to the elevated position on the side of the neural arch on the tenth (considered the first dorsal), agrees with the conditions found in *C. browni* and in the holotype of *C. dispar.*

The odontoid is all that remains of the atlas. The axis, which lacks a portion of the spinous process, is otherwise very similar to the same bone in *C. dispar.* The second, or axis intercentrum, is not co-ossified as in the other species. In the narrowness of the ventral keel and the deep lateral depressions on the sides of the centra the remaining cervicals appear to approach the vertebræ of *C. browni*

[a] Marsh's original accession number is |1561|. No. 1881 is the number under which this specimen was catalogued while in the Yale University Museum.

[b] Bull. No. 179, U. S. Geol. Surv., p. 501. Hay gives the locality as Wyoming (?). On the original field labels found with the specimens the locality was given in full, and may now be considered as absolutely determined.

rather than those of *C. dispar*. The opisthocoelian nature of the anterior vertebræ is not so pronounced as in the larger species.

The dorsal series, though all are not articulated, appears to be complete, consisting of 16 vertebræ, many of which lack parts of their processes. The only marked characters in the dorsals of *C. nanus* are to be seen in the spinous processes of the posterior portion of the series, which are comparatively thin and lack the enlarged upper extremities of the same vertebræ in *C. dispar* and *C. browni*. The arches also appear to be relatively higher, with a corresponding enlargement of the neural canal, in this respect approaching *C. prestwichii*. The sides of the centra (considered as a whole) are less concave in the longitudinal direction and appear to be more evenly rounded ventrally. The centra gradually increase in length from the first to the thirteenth, the fourteenth being the shortest of the posterior dorsals (26 mm.). The fifteenth and sixteenth dorsals may be distinguished from the others by the enlargement of their posterior ends in adaptation to the corresponding surfaces of the centra with which they articulate. The sixteenth or sacro-dorsal (see *S. dor.*, fig. 39) is suturally united with the centrum of the first sacral. Its ventral surface lacks the decided keel found in the sacro-dorsal of *C. browni*. The more detailed description of this vertebræ and the succeeding sacrals will be found in that part of the present paper relating to the osteology of *Camptosaurus*, pages 242 to 244. The sacral vertebræ show the most distinctive character of the species in the absence of the peculiar peg-and-notch articulation of the centra, which forms an important feature of the larger species. By some this difference might be considered of more than specific importance, but on account of the close similarity (except in size) of nearly all of the other elements to the homologous parts of the larger species, and the lack of other diagnostic characters, I can see no reason for separating this form generically. It is of interest to note the similarity in this respect of *C. nanus* to *C. prestwichii* as described and figured by Hulke (see fig. 43).

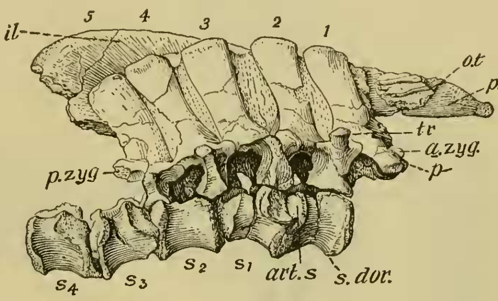


Fig. 39.—Sacrum of Camptosaurus nanus Marsh. Cat. No. 2210, U.S.N.M. ¼ nat. size. Holotype. Viewed from the right side. *a. zyg.*, prezygapophyses; *art. s.*, articular surface for first sacral rib; *il.*, ilium; *o. t.*, ossified tendons; *p.*, parapophysis of the fifteenth dorsal; *p. il.*, preacetabular process of ilium; *p. zyg.*, postzygapophyses; S^1, S^2, S^3, S^4, sacrals one to four, respectively; *tr.*, transverse process or diapophysis; *1*, spine of fifteenth dorsal; *2*, spine of sixteenth or sacro-dorsal; *3*, *4*, and *5*, spines of sacrals one, two, and three.

Most of the caudal vertebræ are articulated, the first alone of the anterior ones being detached, but its size and other characteristics at once show its proper place in the series. So closely do they resemble the caudals of *C. browni*, described elsewhere, that I shall mention only a few of their important features.

The second caudal bears the first chevron. As in *C. browni*, transverse processes are developed on the first thirteen vertebræ, counting back from the last sacral, where they stop abruptly. As shown by some of the detached transverse processes, they are united to the vertebræ by suture, about equally with the upper lateral surface of the centrum and the lower lateral surface of the pedicle of the neural arch. This would appear to indicate ossification from a separate center and would also suggest the appropriateness of calling them caudal ribs, as is done by some anatomists. A distal caudal preserved exhibits the usual long, slender, pre- and postzygapophyses. The important measurements of the vertebræ will be found in the table on pages 242 to 244.

FIG. 40.—RIGHT SCAPULA AND CORACOID (REVERSED) OF CAMPTOSAURUS NANUS MARSH. CAT. NO. 2210, U.S.N.M. HOLOTYPE. ½ NAT. SIZE. FROM A PHOTOGRAPH.

The right fore limb, lacking most of the foot, is preserved with this specimen, and is the one on which Marsh based his restoration of the limb of *C. nanus*, first published [a] in July, 1894, the foot there shown being drawn after that of *C. dispar*, No. 1877, Yale Museum.

The scapula, as will be observed by comparing it with the same elements of the larger species (as shown in fig. 23), shows no appreciable differences, except in its much smaller size. Thus, as will be seen, *C. nanus* can not be distinguished by its "long sigmoid scapula," as first defined by Marsh, he being led into this error by a wrong interpretation of the missing upper part of the scapula of the typical specimen of *C. dispar*, of which he attempted a restoration at the time of describing the present species.

The coracoid, as compared with the same element of *C. dispar* and *C. browni*, is shorter antero-posteriorly, more quadrangular in outline, with a proportionately deeper notch on the inferior border.

The foramen is not closed, as represented in Marsh's figure, but, as in the other forms, is a notch, being open to the articular border for

[a] Amer. Jour. Sci., XLVII, pl. 5, fig. 3.

the scapula. In the type-specimen the coracoid and scapula were not coossified. (See fig. 40.)

The humerus lacks the robust development of the deltoid crest and the articular ends are not so rugose as in the larger species; in other respects they appear identical (compare figs. 25, 26, and 41).

The ulna (see *ul*, fig. 41) appears to be more curved than the ulnæ of either *C. browni* or *C. dispar*, but in the triangular contour of the proximal end it approaches the latter species. The radius shows no important differences.

Both of the ilia were recovered and, as found, were not far removed from their normal position in relation to the sacrum, as shown in fig. 39, the left one being the more complete. In its general proportions it approaches the ilium of *C. dispar* (see Plate 14, fig. 2) rather than the narrow and more depressed ilia of either *C. medius*, *C. browni*, or *C. depressus*, although the anterior termination of the preacetabular process is especially like that of the latter species. The acetabular notch is deep and the ischiac process robustly developed, and there is a wide horizontal plate or shelf on the inner side of the posterior portion, as in the larger species. The pubic process is directed forward and well downward, thus giving good width to the preacetabular notch.

FIG. 41.—RIGHT HUMERUS, RADIUS AND ULNA CAMPTOSAURUS NANUS MARSH. CAT. NO. 2210, U.S.N.M. HOLOTYPE. ½ NAT. SIZE. *h*, HUMERUS; *ra*, RADIUS; *ul*, ULNA. FROM A PHOTOGRAPH.

The ischia of *C. nanus* lack their distal ends, but a comparison of the remaining parts with those of the larger species shows no especial differences. The portion of a pubis pertaining to the type is too mutilated to allow of accurate comparison, although it shows that a postpubic process was present.

Except in their very much smaller size, a critical comparison of the elements of the hind limbs of *C. nanus* with those of *C. dispar* failed to reveal any essential differences. Ossified tendons still adhering to the vertebræ, and particularly to the sacrum, were found in the matrix (see *o. t*, fig. 39).

After a careful review of the typical material, as compared with the other species of this genus, I find that *C. nanus* may now be characterized as follows:

Specific characters.—Typically of small size. Coracoid short, quadrangular in outline. Sacral vertebræ without peg-and-notch articulation.

That the type-specimen represents an adult individual there appears to be but little question. While the sutures on the vertebræ are plainly discernable, nearly all of the arches remain attached to their centra, while in some of the larger species we find them wholly

FIG. 42.—(1) RIGHT FEMUR CAMPTOSAURUS NANUS MARSH. CAT. NO. 2210, U.S.N.M. HOLOTYPE. ½ NAT. SIZE. INTERNAL VIEW. (2) FRONT VIEW OF SAME. *a*, LESSER TROCHANTER; *b*, INNER TROCHANTER; *h*, HEAD. FROM A PHOTOGRAPH.

detached. If a young individual, it is of interest to note the presence of ossified tendons in an immature animal, a condition hardly to be expected.

Principal measurements of Camptosaurus nanus.

	mm.
Greatest length of left ilium	244
Greatest vertical height over ischiac process	82
Greatest vertical height over pubic process	77
Greatest vertical height middle of acetabulum	45
Combined length of four sacral centra	126
Greatest length of femur	258
Greatest width of proximal end of femur	72
Greatest width of distal end of femur	71
Greatest length of tibia	235
Greatest width of proximal end of tibia	83
Greatest width of distal end of tibia	79
Greatest length of fibula	207
Greatest width of proximal end of fibula	47
Greatest width of distal end of fibula	26
Greatest length of scapula	187
Greatest width of articular end	53
Greatest width of free end	59
Greatest length of coracoid	35
Greatest width of coracoid	49
Greatest length of humerus	143
Greatest width of proximal end of humerus	43
Greatest width of distal end of humerus	30
Greatest length of ulna	102
Greatest width of proximal end of ulna	26
Greatest width of distal end of ulna	21
Greatest length of radius	45
Greatest width of proximal end of radius	16
Greatest width of distal end of radius	15

Measurements of the vertebræ of this specimen will be found in the table of comparative measurements given on pages 242 to 244.

CAMPTOSAURUS PRESTWICHII (Hulke).

Iguanodon prestwichii HULKE, Quart. Journ. Geol. Soc. London, XXXVI, 1880, pp. 433–454, pls. XVIII–XX, figs. 3–5.

Cumnoria prestwichii SEELEY, Rep. Brit. Ass. for 1887 (1888), p. 698.

Camptosaurus prestwichii LYDEKKER, Cat. Foss. Reptilia and Amphibia Brit. Mus., Pt. 4, Suppl., 1890, p. 259; Quart. Journ. Geol. Soc. London, XLV, 1899, pp. 47, 48.

Camptosaurus prestwichii NOPCSA, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Holotype.—Preserved in the Museum at Oxford, England; collected from the Kimeridge Clay of Cumnor-Hurst, Oxfordshire, England. Consists of a fairly complete skeleton, of which the following elements are preserved: Parts of the posterior region of the skull, portions of the parietals, frontals, and postfrontals, both mandibular rami, portions of both maxillæ; 64 centra, of which 7 are considered cervical, 18 dorsal, 4 sacral, and 35 caudal; portions of both ilia, fragments of the pubes, and 1 ischium. The limbs are represented by the articular ends of the femora, tibiæ, and fibulæ; tarsals, metatarsals, and phalanges; portions of the scapulæ, humeri, and metacarpals.

In the original paper, Hulke gives a detailed description of the skeletal parts of the holotype. The article in question is of too great length, however, to be wholly incorporated in the present paper, and I shall confine my remarks to a brief review of the chief characteristics, as described and figured by Hulke, in comparison with those of the American species.

Review of the typical material.—The occipital condyle has the same reniform outline and forward development of the articular area on the ventral surface as found in the American species. Its union with the basisphenoid by a median tongue of bone received in a corresponding notch on the posterior end of the latter element, and the pronounced winding grooves on the lower and lateral surfaces of the basisphenoid which marks the course of the internal carotid artery, are similar to those in *C. dispar*. The exoccipitals are perforated by the usual foramina, and, as in *C. dispar*, these bones enter slightly into the formation of the occipital condyle. The supra-occipital contributes to the upper boundary of the foramen magnum, its outline and relationship to the surrounding elements appearing identical with the same bone in *C. dispar*, as shown in fig. 4. The parietal bone is single, the median crest sharper than in either *C. medius* or *C. dispar*. The frontals are short and broad, and but little, if any, of their outer borders enter into the formation of the orbital cavity. The postfrontal has a smooth orbital surface of great extent. I am unable to detect any differences which would distinguish the teeth of the upper and lower jaws from those of the American forms. An idea of their size may be gleaned from the following measurements: In a piece of the maxillary, in a space of 75 mm., are the sockets of an outer series of nine teeth. The breadth (that is, antero-posterior dimension) of a fully formed upper crown is 9.5 mm. The greatest breadth of the largest lower tooth crown is 12.5 mm., that of other crowns varying between 10 and 11.5 mm.

Of the twenty-five presacral vertebræ preserved, seven are considered by Hulke as cervical, and, since the atlas and axis are missing, there would be in the complete neck at least nine vertebræ. The opisthocœlous nature of the centra, the presence of the parapophyses on the anterior end of the centra, the deep, lateral depression, and the pronounced median keel, are all characters common to the other members of the genus. But the angularity of the centra, as viewed from the end, is peculiar to this species.

In the anterior dorsals it is apparent from Hulke's description that the transition of the parapophyses from the centrum in the last cervical to the side of the neurapophyses in the early dorsals, and finally to the anterior border of the transverse process in the median dorsal region, approximates the conditions noted in the American species. The presence of 18 dorsals with this specimen raises the question as to the correctness of the vertebral formula of *Camptosaurus*, as determined from a study of the two skeletons, Cat. Nos. 4282 and 2210, U.S.N.M., which agree in having 16 vertebræ, considered as dorsals, in front of the sacrum. If 16 is the correct number for *Camptosaurus*, then *C. prestwichii*, having 18 dorso-lumbars, approaches *Iguanodon* more closely.

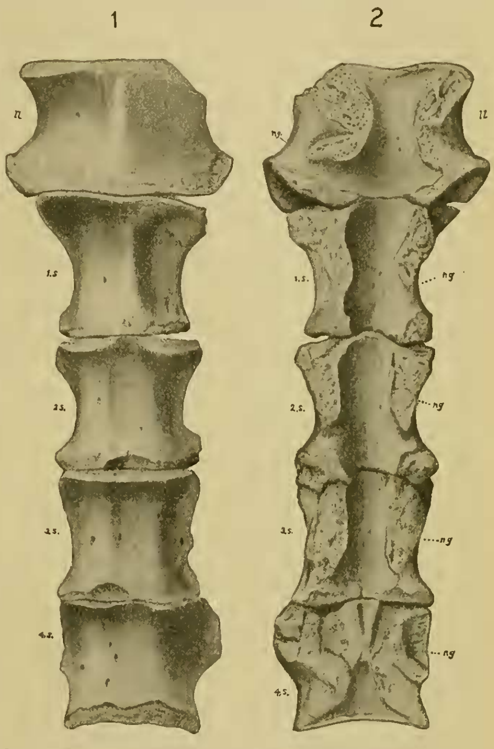


Fig. 43.—(1) The last dorsal or sacro-dorsal and sacrum of Camptosaurus prestwichii (Lydekker), Museum of Oxford. Holotype. Seen from below. $\frac{1}{3}$ nat. size. (2) The same from above; *ll*, sacro-dorsal; *1. s.*, *2. s.*, *3. s.*, and *4. s.*, sacrals one to four, respectively; *ng*, nerve-groove. After Hulke.

In the sacrum, five vertebræ are united by suture, the most anterior of which is considered by Hulke as a lumbar (sacro-dorsal), the posterior four being true sacrals (see fig. 43). While the sacrals do not show the well-defined peg-and-notch articulation of some of the American species, yet, as shown by the figures of this region, there appears to be a tendency toward the development of such an articulation between sacrals one and two, and also between sacrals two and three, much as in *C. nanus*. In the size and number (five) of coossified vertebræ and the contour of their ventral surfaces, the sacrum approaches that of *C. nanus*. It differs, however, in the transversely contracted neural canal of the fourth which also bears the transverse process or last sacral rib wholly upon its centrum. As will be seen in fig. 39, this rib is borne intervertebrally in *C. nanus*. In the transverse contraction of the neural canal of *C. prestwichii*, the fourth sacral resembles that of *C. dispar*, as shown in fig. 37, although, as in *C. nanus*, the rib is supported intervertebrally.

The anterior caudal vertebræ, as described, show the same shortness of centrum, the backward slant of the spinous process, the transverse processes, and the distinctive obliquity of the more anterior ones. As in the American species, the suppression of the transverse processes is soon followed by the disappearance of the neuró-central suture. The median caudals are compressed and the more distal ones have a simple, cylindrical form.

The change in form of the articular surfaces of the vertebral centra, traceable through the column, when compared with the American species, is highly instructive. In the neck these surfaces are opisthocœlous; at the root of the neck, the anterior ball is less convex, the posterior cup less deep; in the forward dorsal region, the anterior surface is very slightly concave, the posterior surface more so, and in the tail, both surfaces are concave.

Such parts of the ilia as are preserved apparently lack the horizontal plate developed in all of the American species. Its absence, however, may be due to the mutilated condition of the bones. The pubis and ischium were too fragmentary for description.

The femora were represented by portions of the articular ends. The presence of a deep, narrow, anterior intercondylar notch characteristic of the Wealden iguanodonts, is quite different from the broad, comparatively shallow groove found on the femora of *Camptosaurus*. The tibiæ, which are also imperfect, show no important differences.

The tarsus consists of two elements, astragulus and calcaneum, which, as in the American species, remain distinct, and appear quite similar in nearly all respects. There were no elements found which could be identified as pertaining to the distal row of the tarsus.

As described, the foot elements show no particular differences from the American species, except in the lateral compression of the unguals, those of the American species, with the exception of the first, being somewhat depressed.

Some imperfect bones, which were more slender and appeared to have been relatively longer than the metatarsals, Hulke regarded as metacarpals. These are suggestive of an iguanodont rather than a camptosaurian type of animal.

The other elements preserved are all too fragmentary to admit of comparison.

The specimen, as briefly reviewed above, was first described by Hulke as a new species of *Iguanodon*, being separated from its nearest ally, *I. mantelli*, by the following characters: "The flattening of the undersurface of the sacral centra, and the relative simplicity of the marginal serrature of its teeth." Later, Seeley proposed the genus *Cumnoria* for the reception of this fossil, characterizing it as follows: "It is separated from *Iguanodon* by many characters, such as the different type of the parallel ridging and coarser serration of the teeth. The vertebræ are relatively wider, the neural arch and centrum both being more depressed; the lamina of the neural arch are very stout, and the neural canal very small; the sacral vertebræ are not ankylosed, are only four in number, and are convex on the ventral surface. The early caudal vertebræ are reduced in length, and have the neural arch small. The astragulus and calcaneum are separate."

In 1899, Lydekker referred the species to *Camptosaurus*, thus relegating *Cumnoria* "to the rank of a synonym till it can be shown to have well-marked distinctive features." He further says: "Evidence of affinity between that species [*Cumnoria* (*Iguanodon*) *prestwichii*] and *Camptosaurus* is shown by the angulated and flattened hæmal surface of the sacral vertebræ, and by the absence of ankylosis between the centra."

Hulke believed the typical specimen to represent an animal between 10 and 12 feet in length, but not fully adult.

While the foregoing review of the description and figures of *C. prestwichii*, as compared with the homologous parts of the American species, show many points of resemblance, certain differences which have been pointed out show a closer relationship to *Iguanodon* than to *Camptosaurus*. The acquisition of better-preserved specimens may eventually show the generic distinctness of this form; but at the present time I fail to detect characters of sufficient importance to warrant its separation. For the present, *C. prestwichii* may be distinguished as follows:

Specific characters.—Typically of moderate size; centra of cervical vertebræ subrhombic in outline. Sacrum of four vertebræ without peg-and-notch articulation. Femur with deep, narrow, intercondylar notch. Unguals of pes compressed laterally. Metacarpals slender and relatively longer than metatarsals.

CAMPTOSAURUS? LEEDSI Lydekker.

Camptosaurus leedsi Lydekker, Quart. Journ. Geol. Soc. London, XLV, 1889, pp. 46–48, fig. 3.

Camptosaurus leedsi Nopcsa, Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Holotype.—A fairly complete femur from the left side, now preserved in the collection of Mr. A. N. Leeds, of Eyebury, England. From the Oxford Clay, near Peterborough, England.

Description.—No characters of specific importance were given by Lydekker to separate this species from the other forms under this genus. For the present I can do no better than to quote Mr. Lydekker's original comments.

The present middle portion of the shaft has been considerably crushed and broken, but both extremities are entire. The shaft agrees with the femur of

Hypsilophodon and of the North American *Camptosaurus* (*Camptonotus*), and differs from that of *Iguanodon* in its markedly forward arcuation. The inner trochanter has lost its free extremity, but the basal portion shows that it is of the "pendant" type characteristic of the two former genera and not the "crested" type found in *Iguanodon*. The anterior intercondylac groove is slightly less developed in this specimen than in either of the Wealden genera, but it is still present. * * * There is, indeed, no decisive evidence to prove that the present specimen indicates a form specifically distinct from the species from the Kimeridge Clay [*C.* (*Iguanodon*) *prestwichii*]; but since most of the Sauropterygians of the Kimeridge are distinct from those of the Oxford Clay, I think it highly probable that the same may hold good with the Dinosaurs, and I therefore propose to provisionally regard the present specimen as the representative of a distinct species which may have been somewhat smaller than *Iguanodon prestwichii*, * * * and since I can see no characters by which either this specimen or *I. prestwichii* can be separated from *Camptosaurus*, I propose to refer both the Kimeridgian and Oxfordian species to that genus under the respective names of *C. prestwichii* and *C. leedsi*.

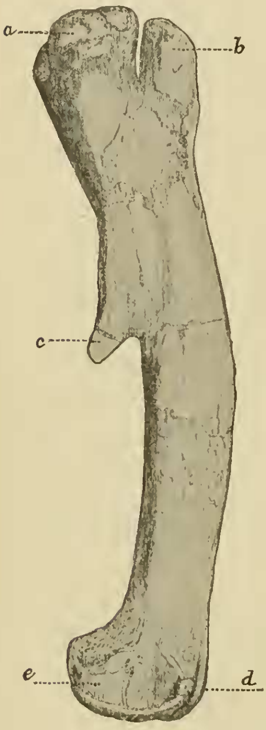


Fig. 44.—Left femur of Camptosaurus leedsi Lydekker; from the Oxford Clay near Peterborough. ⅓ nat. size. Holotype. *a*, head; *b*, lesser trochanter; *c*, inner trochanter; *d*, intercondylar groove; *e*, inner condyle. After Lydekker.

While the femur of *C. leedsi*, as described and figured by Lydekker, appears similar in most respects to the femora of the American *Camptosaurus*, yet the position of the inner trochanter wholly upon the proximal half of the shaft (see fig. 44) at once distinguishes it from all of the described species of that genus, which in all cases show this trochanter extending somewhat below the median line. That *C. leedsi* represents a closely related form there can be no question, but, if referable at all to an American genus, its closest affinities, as indicated by the femur, are with *Dryosaurus*. This suggestion becomes more apparent when it is known that a recent examination of the type specimen of *D. altus*, No. 1876, Yale Museum, shows that the femur has been incorrectly illustrated. For example, the shaft is not straight, but is curved as in *Camptosaurus*, and while the inner trochanter is upon the proximal half, it is not placed so high as indicated in the figure.[a] The femur of *C. leedsi* may be distinguished from the femur of *Hypsilophodon* by the "more wing-like" shape of the inner trochanter of the former.

[a] Amer. Journ. Sci., XVI, 1878, pl. IX, fig. 3.

CAMPTOSAURUS? VALDENSIS Lydekker.

Hypsilophodon LYDEKKER, Cat. Foss. Reptilia and Amphibia. Brit. Mus., Pt. 1, 1888, pp. 195, 227; Geol. Mag., Dec. 3, V, 1888, p. 453.

Camptosaurus valdensis LYDEKKER, Quart. Journ. Geol. Soc. London, XLV, 1889, p. 48.

Camptosaurus valdensis NOPCSA, Földstani Közlöny, Budapest, XXXI, 1901, p. 210.

Holotype.—No. R. 167, British Museum; an imperfect femur, from the Wealden of the Isle of Wight. With this Lydekker provisionally associates a mandibular ramus, No. R. 180.

Lydekker[a] records this femur as pertaining to the genus *Hypsilophodon.* Later he says:

It is not improbable that the mandibular ramus entered on p. 227, Cat. of Fossil Reptilia and Amphibia of the British Museum, as a young Iguanodont, may really indicate a smaller adult form, allied to *Laosaurus* or *Camptosaurus*, in which event the undetermined femur mentioned on p. 195 may perhaps belong to the same form.

A year later he comes to the following conclusion regarding the disposition of these specimens:

I have called attention to an imperfect femur in the British Museum (No. R. 167) from the Wealden of the Isle of Wight, which has been referred to *Hypsilophodon*, and have suggested that, together with a mandibular ramus (No. R. 180) from the Wealden, hitherto regarded as that of a young *Iguanodon*, it probably indicates a form allied to *Camptosaurus*. A comparison of this femur with the subject of the present communication [*C. leedsi*], shows such a close similarity between the two that there is every probability of their generic identity; and since there is no other evidence of the existence of a *Hypsilophodon* of these dimensions, I propose to apply the name *Camptosaurus valdensis* to the Wealden form, of which I take the femur as the type, and provisionally associate with it the mandibular ramus.

Since the type femur has not been described nor figured, a comparison with the femora of American forms can not be made at this time, but, inasmuch as its resemblance to the typical femur of *C. leedsi* was the chief reason for assigning it to this genus, there is every probability that this form is also distinct from *Camptosaurus*. The fragmentary nature of the material upon which the species is based precludes the possibility of ever defining it adequately, and it will probably always remain a species of uncertain affinities.

CAMPTOSAURUS? INKEYI Nopcsa.

Camptosaurus inkeyi NOPCSA, Denkschr. k. k. Akad. Wien, LXVIII, 1899 (1900), p. 579; Földtani Közlöny, Budapest, XXXI, 1901, p. 210.

Holotype.—Dentary and a fragment of the angular from the Upper Cretaceous of Transylvania (Comitat Hunyad), Hungary.

[a] Catalogue of Fossil Reptilia and Amphibia in the British Museum, p. 195.

The original preliminary description of this species, which appears as a footnote in Nopcsa's paper on *Limnosaurus transsylvanicus* in the publication cited above, is as follows:

Camptosaurus inkeyi new spec. (nach Herrn Béla Inkey ehemaligen Chefgeologen der k. ung. geol. Anstalt als Zeichen meiner Dankbarkeit für die zahlreichen Winke, durch die er mir das Studium der geologischen Verhältnisse des Hátszegerthales wesentlich erleichterte). Nur Dentale und ein Fragment der Angulare erhalten. Partie bei der Symphyse *dreikantig* und auf spitzen Schnabel hinweisend. Keine eigene Symphysenfläche, sondern die Kieferspitze innen und aussen rauh sculpirt, was auf ligamentöse Verbindung deutet. Foramen mentale vorhanden. Eine darüber gelegene Rinne (wie bei den Iguanodontiden) fehlt. Ober- und Unterrand des Kiefers nicht parallel. Unterrand etwas gekrümmt wie bei *Hypsilophodon* (Hulke 1882). Innerand bei den Alveolen gleich hoch mit dem Aussenrand. Die interne Rinne und die Foramina (10) sehr stark entwickelt. 10 Alveolen. Zähne ähnlich wei bei *Camptosaurus*, jedoch regelmässiger gekerbt. Ohne bemerkenswerthen Mediankiel. Eine detaillirtere Beschreibung soll bei einer anderen Gelegenheit gegeben werden.

From the above description it is at once apparent that the dentary of *Camptosaurus inkeyi* is quite unlike those of the American species, so far as known. In *C. dispar*, as shown in fig. 8, the outer and inner surfaces of the anterior end of the dentary are reasonably smooth; the upper and lower borders parallel, the ventral nearly straight, curved slightly if at all; internal alveolar border lower than external; fifteen to sixteen alveoli; teeth with one or more prominent and many secondary longitudinal ridges. A comparison of these characters with those described by Nopcsa shows but few in common. These appear to be in the presence of the foramen mentale, the curved teeth, and the presence of a longitudinal groove below the internal alveolar border pierced by the foramini, the latter, however, being more numerous in the American species.

The wide differences shown in the above brief review appear to indicate at least the generic distinction of the form under consideration, but since Nopcsa has promised a more detailed description of his specimen, I shall leave the matter to him for final disposition.

CAMPTOSAURUS DEPRESSUS, new species.

Camptosaurus Lucas, Proc. U. S. Nat. Mus., XXIII, No. 1224, p. 591.

Holotype.—Cat. No. 4753, U.S.N.M. Collected by Mr. N. H. Darton, of the U. S. Geological Survey, in "Calico Canyon," near Buffalo Gap Station, South Dakota, from beds considered by him to be of Lower Cretaceous age (Lakota sandstone).

The type specimen consists of portions of both ilia, anterior part of the blade of one pubis, an incomplete sacrum, centrum of the last or sacro-dorsal, 12 caudal vertebræ, 1 thoracic rib, and many fragments. This specimen was associated with the fragmentary skeleton, No. 4752, U.S.N.M., described by Dr. F. A. Lucas as *Stegosaurus* *marshii*[a] and later referred by him to the new genus *Hoplitosaurus*.[b] Most of the elements preserved were inclosed in two large pieces of rock.

The distinctive characters shown by the ilia, sacrum, and pubis appear to justify the establishing of a new species, for which I propose the name *Camptosaurus depressus*, the specific name being suggested by the narrowness or depressed nature of the ilia.

Specific characters.—Ilium narrow with shallow acetabular and narrow preacetabular notches. Sacrals ankylosed, with rounded ventral surfaces. Anterior end of pubis broad.

FIG. 45.—ANTERIOR PORTION OF RIGHT ILIUM OF CAMPTOSAURUS DEPRESSUS. CAT. NO. 4753, U.S.N.M. HOLOTYPE. ¼ NAT. SIZE. FROM A PHOTOGRAPH.

Detailed description.—The ilium, of which a representation is given in figs. 45 and 46, is characterized by its narrow, vertical depth. The acetabular notch is very shallow and short, while the preacetabular notch is narrow, due to the lower point of origin of the preacetabular process and the more elevated direction of the pubic process, which, in all other species is deflected more ventrally (see Plate 14). Compared with the ilium of *C. browni*, its nearest ally, *C. depressus* appears to indicate a smaller form. The interval between the pre- and post-acetabular notches is comparatively short, measuring 141 mm., while in *C. browni* it is 204 mm. The vertical height of the left ilium from the inferior border of the middle of the acetabulum, allowing for slight crushing, is about 105 mm. As shown by the anterior portion of the right ilium (see fig. 45), the long, curved

FIG. 46.—LEFT ILIUM OF CAMPTOSAURUS DEPRESSUS. CAT. NO. 4753, U.S.N.M. HOLOTYPE. ¼ NAT. SIZE. PREACETABULAR PROCESS WANTING, AND THE UPPER POSTERIOR PORTION IS CRUSHED DOWN SOMEWHAT FROM ITS NORMAL OUTLINE. FROM A PHOTOGRAPH.

[a] Proc. U. S. Nat. Mus., XXIII, 1901, p. 591, pls. XXIII, XXIV.

[b] Science, XVI, Sept. 12, 1902, p. 435.

preacetabular process is terminated by a somewhat more angularly pointed end than the rounded, more spatulate type found in *C. dispar* (see fig. 29). With the exception that the ischiac process is not so robust, in nearly all other respects the ilia appear very similar to those of the better known species. The contour of the posterior end, due to the damaged condition of both elements, can not be determined at this time.

FIG. 47.—ANTERIOR PORTION OF RIGHT ILIUM OF CAMPTOSAURUS DEPRESSUS. CAT. NO. 5820, U.S.N.M. ½ NAT. SIZE. FROM A PHOTOGRAPH.

Turning now to the sacral and caudal vertebræ associated with the ilia, it may be observed that the sacrals are characterized by the ankylosis of all their centra and their quite evenly rounded hæmal surfaces, there being just the faintest indication of the presence of a median keel upon Sacrals I, II, and III. None shows the flattened ventral surfaces observed in the paratype of *C. dispar*, No. 1877*a*, Yale Museum. In this respect, except in size, they more nearly resemble the sacrals of *C. nanus*.

From the fragmentary evidence, it appears there were at least seven vertebræ ankylosed by their centra in this region, the most anterior of which is a sacro-dorsal, the posterior one likely representing a sacro-caudal, as in *C. browni*. Attached to the rock, which also holds the left ilium, are a number of spinous processes, which, if they pertain to the sacrum, show the spines as being much narrower antero-posteriorly, and without the heavy expanded tops of *C. dispar*.

The caudal centra show no distinctive characters, but, as in the other species, the anterior caudals show the same obliquity of the centrum, the small neural canal, the wide transverse processes, and the slightly biconcave cupping of the articular ends. The diameter of the anterior caudal centra is greater vertically than transversely. One of the sacro-caudals shows it to have had a transverse process whose greatest width, at the point of origin at least, is in the vertical direction. The more distal caudal vertebræ, of which there are three present, show the same cylindrical shape, with long pre- and post-zygapophyses, as found in *C. browni.*

The principal dimensions of the holotype are as follows:

	mm.
Vertical depth of ilium from middle of acetabular border (estimated)	105
Distance between pre- and post-acetabular notches	141
Width of pubis 63 mm. from the anterior end	105
Greatest length of sacro-dorsal	58
Greatest length of first sacral	53
Greatest length of second sacral	56
Greatest vertical depth of sacro-dorsal (anterior end)	70
Greatest length of caudal centrum bearing chevron (second?)	51
Greatest width anterior end of caudal centrum bearing chevron (second?)	66
Greatest height anterior end caudal centrum bearing chevron (second?)	76

A second specimen, Cat. No. 5820, U.S.N.M., consisting of the well preserved anterior portion of a right ilium, collected by Mr. J. L. Kenney from the Morrison beds of the Jurassic, near Como, Albany County, Wyoming, undoubtedly pertains to this species (see fig. 47).

CAMPTOSAURUS BROWNI, new species.

Holotype.—Cat. No. 4282, U.S.N.M. From the Jurassic (Morrison beds), Quarry No. 13, 8 miles east of Como, Albany County, Wyoming. Collected by Mr. Fred Brown during the years 1885 and 1886. Named for the collector, whose discoveries of important fossil specimens have done much to further the science of paleontology.

The typical specimen consists of a considerable portion of the skeleton, and since the elements have been listed on page 203, it appears unnecessary to again enumerate them. As this skeleton is the basis for that part of the present paper devoted to the osteology of *Camptosaurus*, where a detailed description of the bones composing it will be found, it is necessary here to discuss only those characteristics by which it differs from the other known species.

Specific characters.—Ilium of moderate depth, with long pre- and post-acetabular processes; the hinder part especially narrow; superior border slightly convex with oblique posterior portion short. Seven vertebræ, of which five are considered sacrals, united by suture in sacral region. Peg-and-notch articulation confined to the posterior members and extending into the anterior caudals. Anterior sacral vertebræ compressed transversely. Last dorsal with ventral keel. Ischia slender with light expanded distal ends.

Typically the skeleton represents an animal about 16 feet in length, intermediate in size between *C. dispar* and *C. medius.* While it approaches the former more nearly in size, it resembles the latter in the comparative lightness of its skeletal structure.

The cervical vertebræ of *C. browni*, when compared with those of *C. dispar*, show a much narrower ventral keel and deeper lateral depressions. The dorsal region, on account of the lack of material, I am unable to contrast with the other species, excepting *C. nanus*, the dorsals of which may be readily distinguished on account of their small size and the thinness of the spinous processes, which are without decided thickening of their superior terminations.

The last, or sacro-dorsal, has a short but decided ventral keel which at once distinguishes this element from the smoothly rounded hæmal surface of this vertebræ in *C. dispar*, or the faint keeled ones as found in *C. depressus*, *C. nanus*, and *C. prestwichii*.

The sacral region of *C. browni* resembles *C. depressus* most nearly in having seven vertebræ united by suture, of which five are considered true sacrals in the former species. The sacrum differs from *C. dispar* in the increased number of sacral vertebræ, the absence, in the anterior elements, of the peg-and-notch articulation, and its continuance into the caudal region, and by the more compressed and keeled anterior centra. The absence of the peg-and-notch articulation in the sacrals of *C. nanus* and *C. prestwichii* at once separates them from *C. browni*.

Outside of the anterior caudals, as noted above, the other vertebræ of the tail show no distinctive features.

As known at the present time, the ilium is one of the most characteristic bones of the entire skeleton of *Camptosaurus*, and since this element is present in all of the holotypes of the American species, excepting *C. amplus*, it offers a basis of comparison equal in importance to the differences displayed in the several species. The length of the ilium (see fig. 30), which wants the extremity of the preacetabular process, is quite equal to that of the average adult individual of *C. dispar* (see figs. 1 and 3, Plate 14), although its greatest depth is considerably less. The preacetabular process when complete was long, the superior border slightly convex, and the post-acetabular portion long and especially narrow, the angular oblique border of the supero-posterior end being short. Compared with the ilia of the other species, the difference in the form of the hinder half, coupled with its other proportions, would, apart from other evidence, indicate the specific distinctness of its owner. In contour the ilium is intermediate between *C. medius* on the one hand and *C. depressus* on the other, as may be seen by comparing figures. Compared with *C. depressus*, it shows a much wider preacetabular notch, a deeper acetabulum, and a greater depth of the bone as a whole.

The pathological condition of the right ilium of *C. browni* is of interest in showing to what extent the shape of a bone may be modified by external injury. On the posterior half, the comparatively thin, plate-like part of the ilium is divided vertically, the two halves swelling out to form the walls of a cavity which extends downward, emerging on the ventral border. The cavity is longer than wide, measuring on the upper border of the opening 86 mm. in a longitudinal direction and 46 mm. in the transverse, the ventral exit being considerably smaller. As indicated by a deep depression on the dorsal border, the injury was probably received from above.

The exostosis of the bone was greatest on the front side of the cavity where it measures 72 mm. in width. The normal diameter of this part of the ilium, as shown by one of the opposite side, is only 21 mm. A second injury was found on one of the caudal vertebræ near the root of the tail, as indicated by the pathologic condition of the spinous process, which is considerably enlarged and has near its base an elongated opening which perforates the bone. While the wound in the ilium must have been an exceedingly painful one at the time of infliction, it in no way utterly disabled the animal, at least to the extent of leading to its death, for, as shown by the specimens, all of the broken margins of the bone had healed. Although these injuries may have been inflicted by some of its large carnivorous contemporaries, the position of the wounds suggests the idea that this individual was a female who might have received the injuries during copulation.

The ischia of *C. browni* are comparatively slender, and while there is a considerable expansion of their distal extremities, they lack the massiveness of those of *C. dispar*. In the lightness of the structure of these elements, they approach *C. medius* most nearly.

The fore limbs and feet show no distinguishing characteristics. The principal measurements of the vertebræ and other parts will be found in that part of the paper devoted to the osteology of *Camptosaurus*.

GEOGRAPHICAL AND GEOLOGICAL DISTRIBUTION.

In North America, camptosaurian remains have been found in southeastern Wyoming, in Albany and Carbon counties;[a] Colorado, near Canon City, and in the "Garden of the Gods", near Colorado Springs; South Dakota, in Custer County, in the vicinity of Buffalo Gap. Beyond the limits of the United States, specimens which have been referred to *Camptosaurus* have been found in England, Isle of Wight, and Hungary.

All of the American species, with the possible exception of *C. depressus*, are from the Morrison beds (Atlantosaurus beds of Marsh),

[a] In the Journal of Geology, XIII, No. 4, 1905, p. 348, Dr. S. W. Williston reports the occurrence of *Laosaurus* remains in Fremont County, near Lander, Wyoming, in deposits considered lower Cretaceous in age.

of the Jurassic, but Marsh's statement that "they occur in successive deposits of the same general horizon, the smallest species below, the largest above,"[a] can not be verified, and is not borne out by the structural characteristics of the typical specimens. Moreover, as shown by the original field labels still remaining with the type material, *C. dispar*, *C. medius*, and *C. nanus* came from the same quarry (No. 13) and in all probability were found at the same level. Although the holotype of *C. amplus* was found in the same general area, it is from another quarry in a region where it is difficult to trace stratigraphic horizons. It also appears from Marsh's own writings that he was not quite clear as to their stratigraphic positions, for in 1879[b] at the close of his description of *C. amplus*, he says: "The remains of the present species are from a lower horizon in the Jurassic than those described above [*C. dispar*], but within the limits of the Atlantosaurus beds." He thus places the larger species at a lower level, which is contradictory to his later statements.

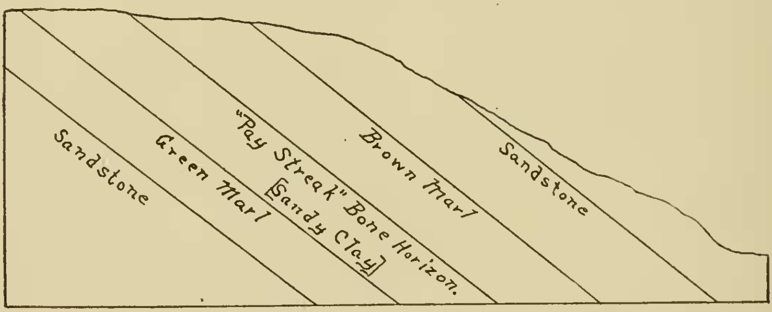


Fig. 48.—Section of Quarry 13. Made by Mr. Fred Brown in 1884.

Since Quarry No. 13 has furnished four of the holotypes pertaining to the genus *Camptosaurus*, besides a vast quantity of other material, the exact stratigraphic position of the bone-bearing layer is of considerable interest. A clue to the position of this layer was found in a rough section of the strata exposed in working this quarry, made by Mr. Fred Brown in 1884 (see fig. 48).

The fossils occur here in a layer of sandy clay,[c] as I have determined from the matrix still adhering to bones, and, as seen in Brown's section, the bone-bearing layer ("pay streak") is intercalated between layers of marl or clay, green below and brownish above, all three layers lying between bands of sandstone.

[a] Amer. Journ. Sci., XLVIII, 1894, p. 85.

[b] Idem, XVIII, 1879, p. 503.

[c] On page 199 of the present paper, Mr. W. H. Reed is quoted as also noting the sandy nature of the matrix in which the fossils occur as being unusual.

In comparing the conditions here with the sections so carefully worked out by Dr. F. B. Loomis[a] at Como Bluff and Little Medicine, in an area a few miles to the west of that under discussion, it appears that this sandy layer may be tentatively correlated with No. 28 of his section (see Plate 20), which he describes as follows:

> No. 28 is a gray sandstone in which the rich Bone Cabin Quarry is situated, and also the Stegosaurus Quarry. The sandstone varies extremely in hardness, being, in the south part of Bone Cabin Quarry, soft and mixed with considerable clay so that it is workable with an awl. In the northern part of the quarry, however, there are bands of the firmest sort of sandstone. In Como Bluff the layer is clay with merely an admixture of sand. Bone Cabin Quarry has yielded a great variety of genera: *Diplodocus, Morosaurus, Brontosaurus, Allosaurus, Ceratosaurus, Camptosaurus, Stegosaurus,* as well as several genera of carnivorous Dinosaurs; also *Compsemys* and *Goniopholis.*

The correctness of the above correlation appears to be indicated (1) by the similar nature, lithologically, of the materials composing the bone horizon, (2) a similarity in the over and underlying strata, (3) the likeness of the faunas from the two localities. If later investigations show this provisional correlation to be correct, it is of the utmost importance as definitely locating the horizon from which the holotypes of the following species have come: *Camptosaurus dispar*, *C. medius*, *C. nanus*, *C. browni*, *Dryosaurus altus*, and *Diracodon laticeps.* Among the other dinosaurian genera recognized from quarry No. 13 are *Stegosaurus*, *Allosaurus*, *Coelurus*, and *Morosaurus*, as well as the turtle, *Glyptops* and the crocodile *Goniopholis*, and fish remains, which, however, are too fragmentary to admit of identification. By comparing the faunal lists of the two quarries, it will be observed that they are quite alike, although Bone Cabin Quarry predominates in representatives of the Opisthocoelia (Sauropoda), Quarry 13 in members of the Orthopoda (Predentata). This observation would also apply to the relative numbers of individuals of each group found in the two quarries. Quarry No. 13, as shown by the maps, was especially rich in stegosaurian and camptosaurian remains.

With the permission of Dr. F. B. Loomis, I reproduce (Plate 20, figs. 1 and 2) sections of the Little Medicine and Como Bluff exposures, which, according to his measurements, show the 5-foot sandy layer No. 28 to be within 60 feet of the overlying Cretaceous (Dakota). This is the highest known horizon of the Jurassic in which camptosaurian bones have been found, and the discovery at this level in the famous "Bone Cabin Quarry" of a skeleton of *C. nanus* (see Plate 19), strengthens somewhat the assumption of the contemporaneity of this layer with the bone horizon of Quarry 13.

[a] Bull. Amer. Mus. Nat. Hist., XIV, 1901, pp. 189–197, pl. XXVII, figs. 2, 3.

The finding of *Camptosaurus* remains in the Lakota, near Buffalo Gap, South Dakota, appears to extend the geological horizon of this genus. The occurrence of these fossils is described by Mr. N. H. Darton[a] as follows:

> The formation has yielded a large number of cycads, notably those described by Mr. Lester F. Ward. These and associated plants are regarded by Mr. Ward as Cretaceous in age. In 1898 I discovered saurian bones in or near the cycad horizon at Buffalo Gap, but as they are of new species it is difficult to obtain from them any evidence bearing on the age of the formation. If it were not for the evidence of the flora, these bones would be regarded as late Jurassic in age. * * * The bone bearing beds are in the middle of the Lakota formation, or about 90 feet above the unconformity on the Unkpapa sandstone which is approximately the horizon that has yielded the cycads between Edgemont and Minnekata, near Blackhawk and elsewhere about the hills.

The vertebrate fauna of the above horizon, as now known, consists of *Hoplitosaurus* (*Stegosaurus*) *marshi* (Lucas) and *Camptosaurus depressus*, new species, while the presence of a sauropodous dinosaur is indicated by some fragmentary bones found associated with the type material.

That the bone-bearing layer at Buffalo Gap is later than the fossil horizon in Quarry 13, Como, Wyoming, appears quite probable, although the evidence as yet is insufficient to conclusively establish the fact. *Hoplitosaurus* has its nearest ally in *Polocanthus* of the Wealden. While the former genus is known by a single fragmentary specimen only, it may, from its geological position, represent a form intermediate between *Stegosaurus* of the Jurassic, and *Nodosaurus*, *Stegopelta*, and *Anchylosaurus* of the American Upper Cretaceous.

Although the typical specimen of *C. depressus* is fragmentary, such parts as are preserved appear to show that of all the known forms of *Camptosaurus* this species approaches the Wealden *Iguanodon* most closely, as indicated by the narrowness of the ilium and the coosification of the sacral vertebræ.

As has been pointed out in the preceding pages, the *Camptosaurus* remains from Quarry 13, when compared with *Iguanodon*, show a more generalized structure, which suggests a somewhat greater antiquity for the beds in which they are found. In this connection it is a significant fact that of the several European species referred to *Camptosaurus*, the only valid one is *C. prestwichii* from the Kimmeridge Clay, and its affinities appear to be nearest to *C. nanus*, the holotype of which was found in Quarry 13. Corroborative evidence is furnished by the abundant remains of *Stegosaurus* found in the above quarry (see Plate 6), which genus is so closely allied to *Dacen-*

[a] 21st Ann. Rept. U. S. Geol. Surv., Pt. 4, 1899–1900, p. 527.

trurus[a] (*Omosaurus*) from the Kimmeridge that Marsh believed them to be identical.

It is unfortunate that the early paleontologists rarely gave any precise location, much less the exact geological horizon from which typical specimens were obtained, so that the faunas of the upper and lower parts of the American Jurassic, except in a few instances, have never been differentiated. The whole fauna has been included under the term Upper Jurassic, and only in the last few years have a few authorities separated some of the upper part as lower Cretaceous. The vertebrates found in the Lakota at Buffalo Gap point to its being the equivalent of the Wealden of England. Assuming, as many authorities do, that the Wealden is really Jurassic, these beds would then represent the uppermost part of that formation.

The above evidence, then, is in favor of the contemporaneity of the Buffalo Gap horizon with the Wealden, and indicates that the age of the Quarry 13 bone layer is greater than the Wealden. Such evidence as is shown by the Camptosauridæ not only supports Hatcher's contention[b] that the lower members of the Morrison (Atlantosaurus Beds) are below the Wealden, but that they are of greater age than the Purbeck and possibly equivalent to the Kimmeridgian.

RESTORATION OF CAMPTOSAURUS.

Marsh gave us the first skeletal restoration of *Camptosaurus*, here reproduced as Plate 18. While this reconstruction gives a good idea of the animal as a whole, it is now known, as has been pointed out earlier in the present article, to be in error in several particulars. The most striking change brought about by this more recent study is the shortening of the presacral region, which was made too long by Marsh, owing to an overestimate of the number of presacral vertebræ. In his figure (see Plate 18) there are 30 presacral vertebræ, 9 of which are considered as belonging to the cervical region, thus leaving 21 thoracic vertebræ. Two specimens in the U. S. National Museum agree in having 16 dorsals each. If, then, this latter number is correct, the presacral series would be shortened by 5 vertebræ, making the proportions of the animal markedly different from the first conception of its appearance (compare with Plate 19). Even though it ultimately be found that *Camptosaurus* has 18 dorsal vertebræ (a possibility indicated by the occurrence of that number in the holotype of *C. prestwichii* and in the allied *Iguanodon*), it would still mean the shortening of the column by 3 vertebræ, which would have lessened the distance between the fore and hind limbs, producing a more compactly built animal than appeared in the first reconstruction.

[a] Science (N. S.), XVI, 1902, p. 435.

[b] Memoirs, Carnegie Musuem, III, 1903, p. 68.

Although there is a considerable disparity in length between the fore and hind limbs, there appears to be some evidence to show that the bipedal mode of progression was not habitual. While I do not wish to be understood as believing that the upright position was not frequently assumed, still it appears to me that the quadrupedal posture was used more frequently than has been generally supposed. This is shown by the compact, ossified carpus, with smooth, well-defined articulating surfaces, which is supported by comparatively short and stout metacarpals, whose function was that of support rather than prehension. When compared with those of animals whose mode of progression is normally bipedal, the suggestion advanced here becomes more apparent. *Trachodon* has slender, elongated metacarpals and imperfectly ossified carpus, and *Iguanodon* also has a tendency toward the lengthening of the metacarpals, though not so marked as in the former genus. The curved femur is also indicative of a flexed limb, which would have equalized somewhat the difference in length between the fore and hind legs. This character of the femur is in striking contrast to the straight femur of both *Iguanodon* and *Trachodon*, a provision, as in the Proboscidæ, for the support of great weight. The obliquity of the anterior caudal centra indicates a rapid dropping of the tail as it leaves the sacrum, which is also suggestive of a normal quadrupedal position. In the two genera mentioned above the caudals extend straight out from the sacrum without appreciable ventral deflection.

Through the courtesy of Dr. W. D. Matthew, of the American Museum of Natural History, I am enabled to present in Plate 19 the first skeleton of *Camptosaurus* to be mounted, which gives a truer conception of the animal than is obtained from the earlier reconstructions. As seen in the figure, the head is comparatively small, being carried on a gracefully curved neck of moderate length. The thoracic region, which has been given 16 dorsals, is of moderate length, borne on stout, clawed limbs, of which the hinder are longer and stouter than the fore. In life this animal was evidently strong and agile in movement. The tail was long, nearly equaling half the total length of the skeleton, and in life it probably served as a balancing organ when the upright bipedal posture was assumed.

Unlike many of the other predentate dinosaurs, there have been no dermal scutes nor ossicles found, so we have no knowledge as to the dermal covering.

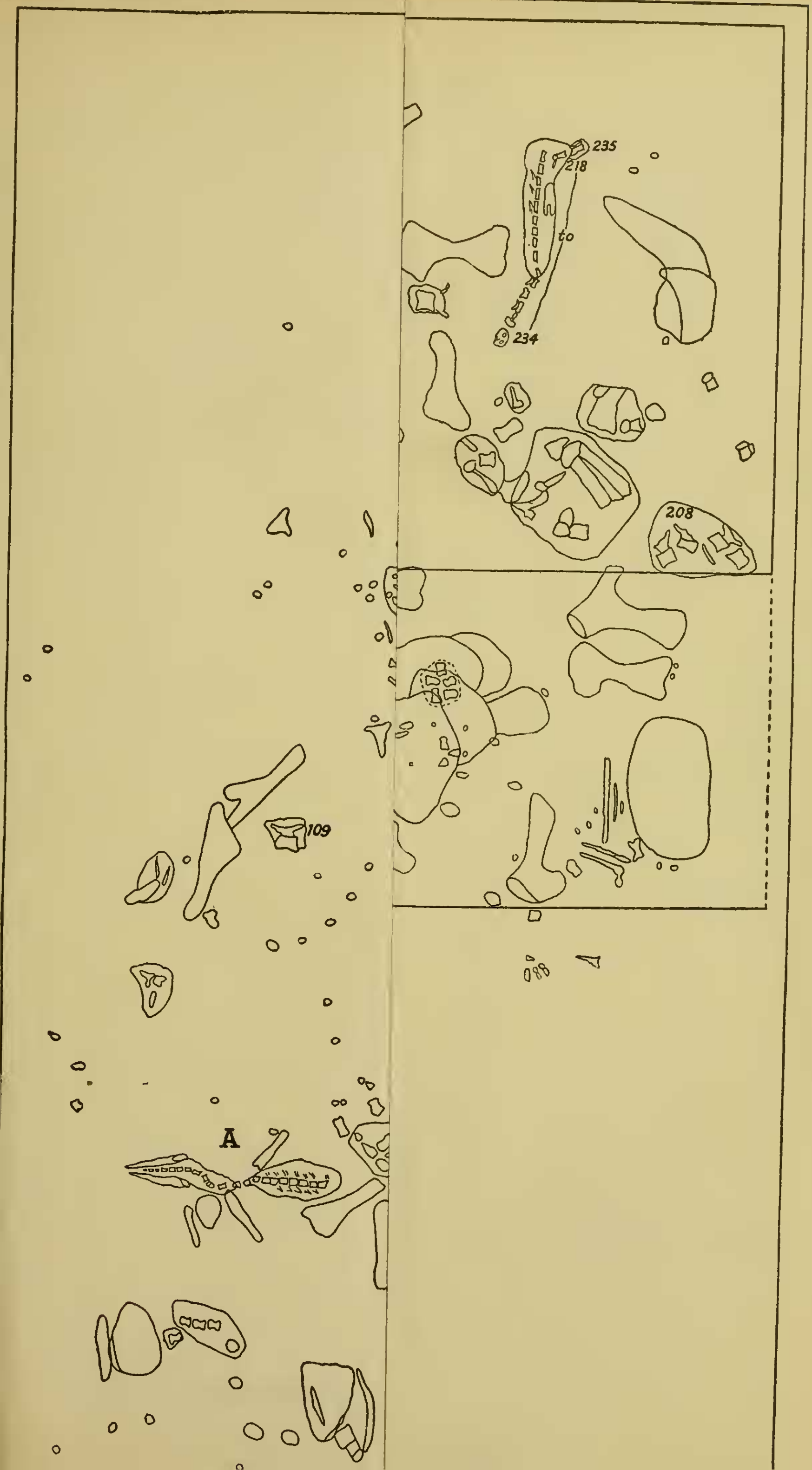
EXPLANATION OF PLATE 6.

Diagrams 5, 7, and part of 4, of Quarry 13, near Como, Albany County, Wyoming, worked by Mr. Fred Brown for Prof. O. C. Marsh, during the years 1884, 1885, and 1886. The numbered bones show the positions in which the various elements of the holotype of *Camptosaurus browni*, Cat. No. 4282, U.S.N.M., were found in the quarry. The unnumbered bones scattered about pertain chiefly to members of the Stegosauria.

A, Plesiotype of *Diracodon laticeps*, Cat. No. 4288, U.S.N.M.

B, Series of caudals and dermal plates of *Stegosaurus*, Cat. No. 4714, U.S.N.M.

The scale is about 4 feet to the inch.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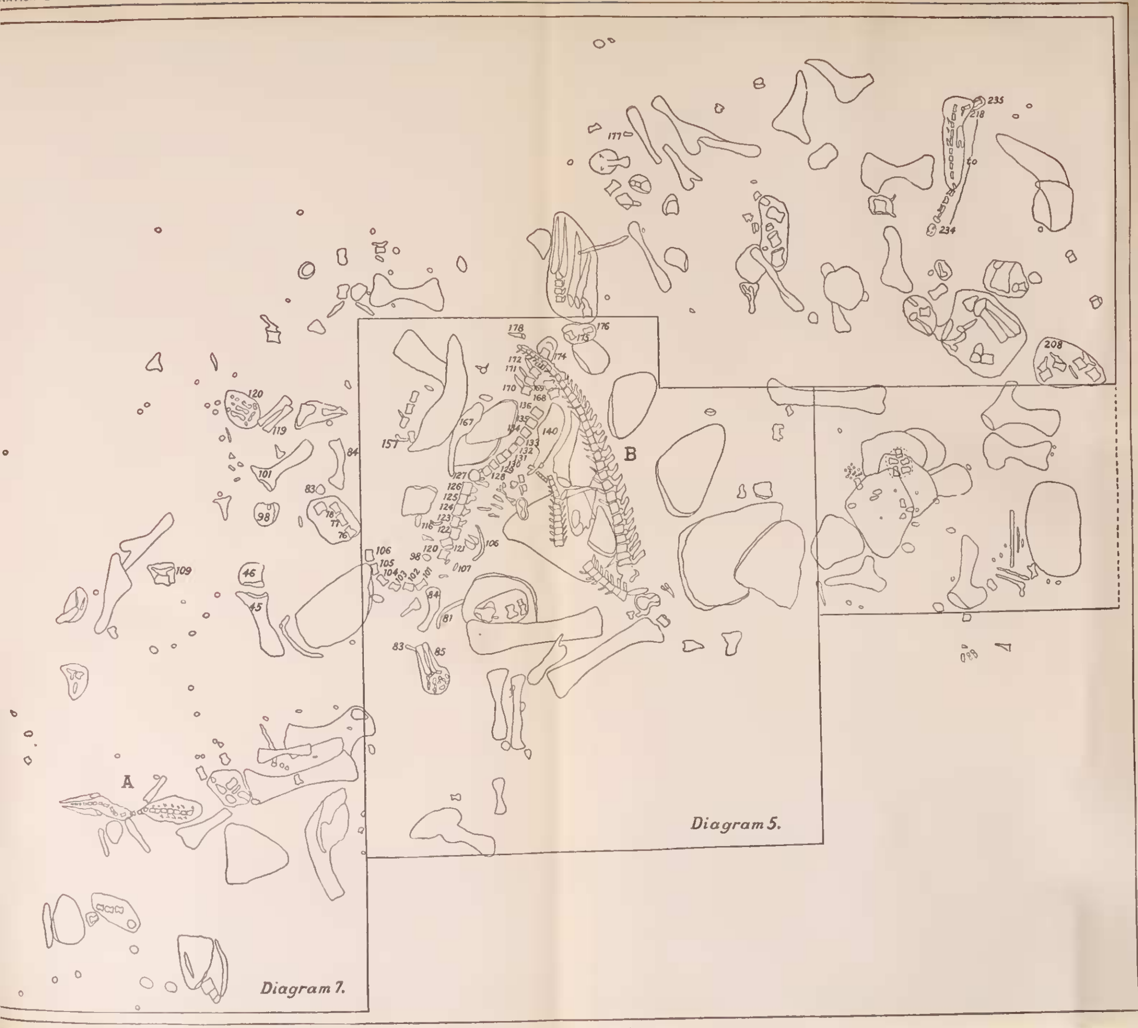


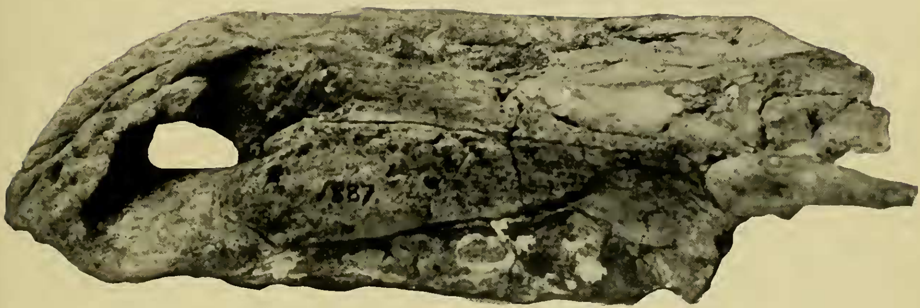
MAP OF QUARRY 13, NEAR COMO, WYOMING.

EXPLANATION OF PLATE 7.

FIG. 1. Anterior part of skull, *Camptosaurus amplus?* Marsh. No. 1887, Yale Museum. About $\frac{2}{5}$ nat. size.

2. Explanatory figure of same: *l*, lachrymal; *m*, maxillary; *na*, nasal; *no*, narial orifice; *pmx*, premaxillary; *prf*, prefrontal; *so*, supraorbital.

1



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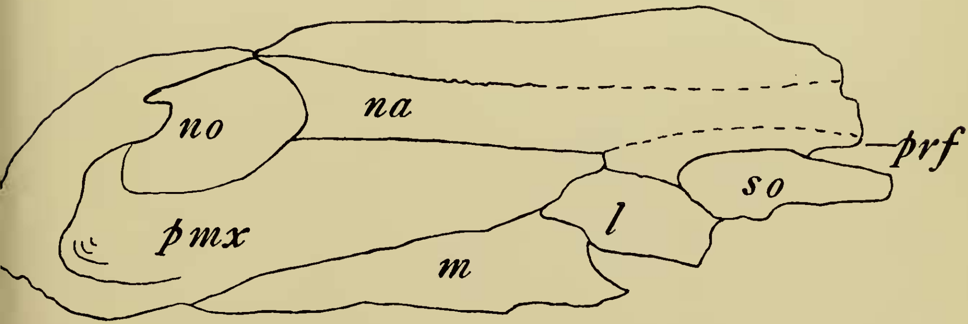


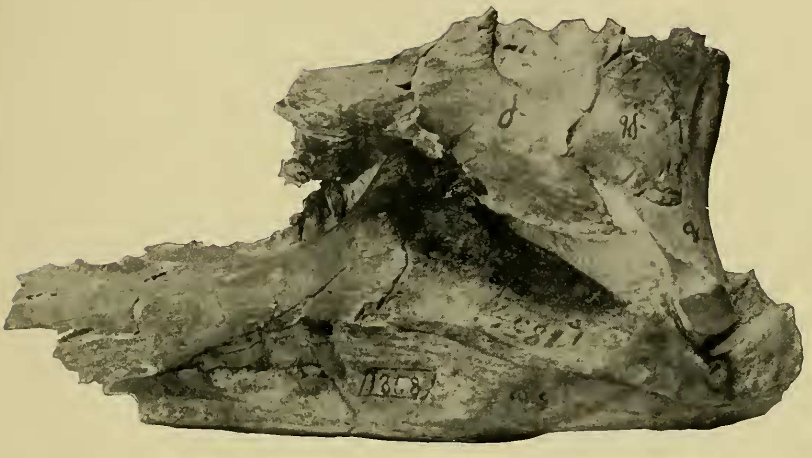
ANTERIOR PORTION OF SKULL OF CAMPTOSAURUS AMPLUS?.

EXPLANATION OF PLATE 8.

FIG. 1. Posterior part of skull, *Camptosaurus amplus?* Marsh. No. 1887, Yale Museum. $\frac{2}{5}$ nat. size. External view.

2. Explanatory figure of same: *ang*, angular; *d*, dentary; *ju*, jugal; *q*, quadrate; *qj*, quadratojugal; *sur*, surangular.

1



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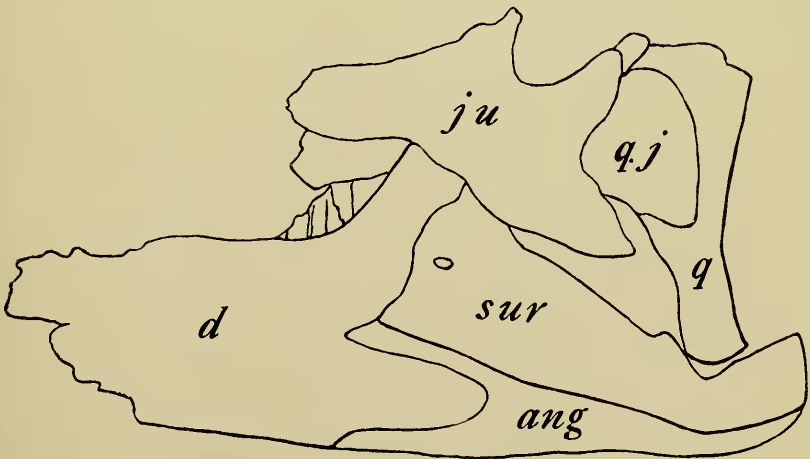


Posterior Part of Skull of Camptosaurus amplus?.

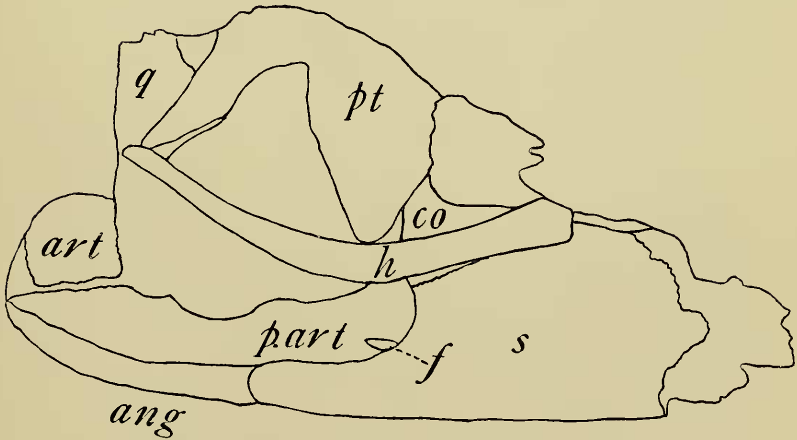
EXPLANATION OF PLATE 9.

FIG. 1. Posterior part of skull, *Camptosaurus amplus?* Marsh. No. 1887, Yale Museum. $\frac{2}{5}$ nat. size. Internal view.

2. Explanatory figure of same: *ang*, angular; *art*, articular; *co*, coronoid; *f*, internal mandibular foramen?; *h*, hyoid; *p*, *art*, prearticular; *pt*, pterygoid; *q*, quadrate; *s*, splenial.

1

2



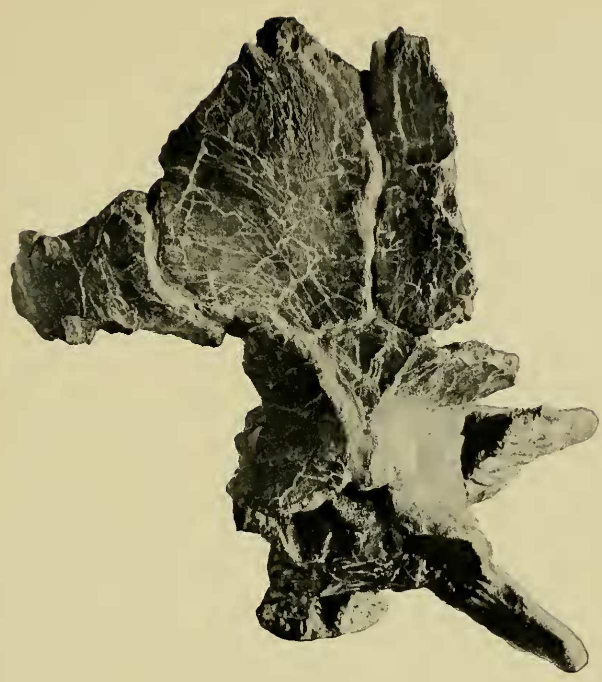
POSTERIOR PART OF SKULL OF CAMPTOSAURUS AMPLUS ?.

EXPLANATION OF PLATE 10.

FIG. 1. Posterior portion of skull, *Camptosaurus dispar* Marsh. Cat. No. 5473, U.S.N.M. ½ nat. size. Seen from above. From a photograph.

2. Explanatory figure of same. *al. sp.*, alisphenoid; *c*, occipital condyle; *f*, frontals; *p*, parietal; *pf*, postfrontal; *poc*, paraoccipital process or opisthotic; *so*, supraoccipital.

1



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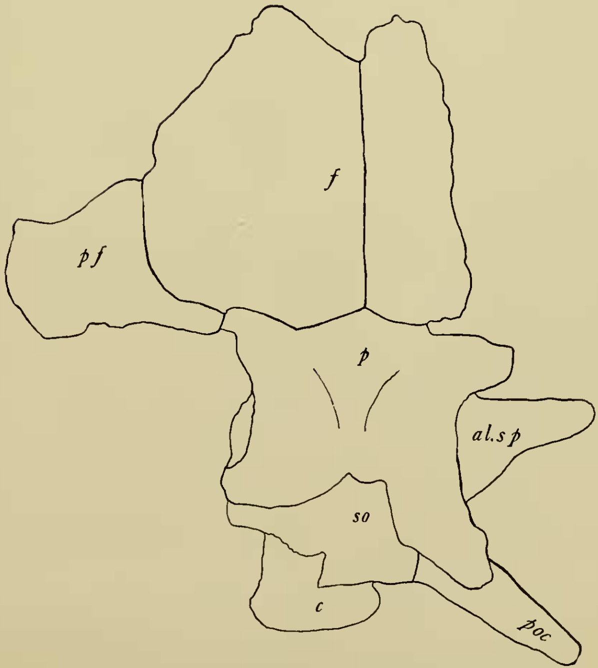


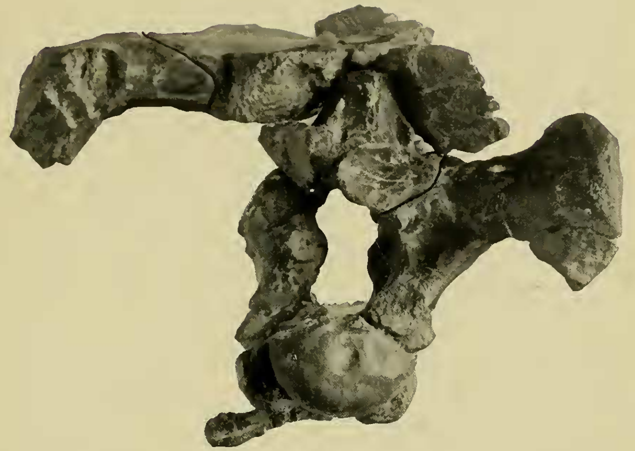
POSTERIOR PART OF SKULL OF CAMPTOSAURUS DISPAR.

EXPLANATION OF PLATE 11.

FIG. 1. Occipital region of skull, *Camptosaurus dispar* Marsh. Cat. No. 5473, U.S.N.M. ½ nat. size. Posterior view. From a photograph.

2. Explanatory figure of same. *bs*, basisphenoid; *exo*, exoccipital; *f*, foramen magnum; *oc*, occipital condyle; *p*, parietal; *pf*, postfrontal; *poc*, paraoccipital process or opisthotic; *p. pt.*, process which meets pterygoid; *so*, supraoccipital.

1



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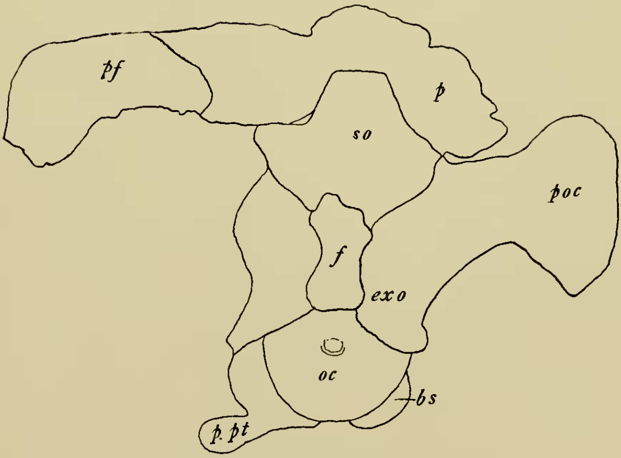

Occipital Region of Skull of Camptosaurus dispar.

EXPLANATION OF PLATE 12.

Complete neck and posterior portion of skull *Camptosaurus dispar* Marsh. Cat. No. 5473, U.S.N.M. $\frac{1}{3}$ nat. size. Viewed from the left side. From a photograph.

NECK AND PART OF SKULL OF CAMPTOSAURUS DISPAR.